PALAEOLIMNOLOGICAL STUDIES ON SEDIMENTS FROM LAKE GRASMERE, SOUTH ISLAND, NEW ZEALAND, WITH SPECIAL REFERENCE TO THE CHIRONOMIDAE (DIPTERA)

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FOR MY FAMILY

AND IN MEMORY OF MY FATHER

CONTENTS

ABSTRACT

Palaeolimnological studies were carried out on a 326 cm long sediment core from Lake Grasmere. The core covered the last 6000 years of the developmental history of the lake. A pollen analysis revealed that Nothofagus pollen was dominant from the base to 30 cm. Above that level an increase in grass pollen indicated the presence of Polynesian people. The European period was represented in the core by the uppermost 6 cm, indicated by the presence of introduced Pinus pollen.

Results of a fossil diatom analysis showed that this fossil flora was dominated by small epiphytic Fragilaria species, the facultative planktic Cyclotella stelligera, and in the youngest sediments by the planktic Diatoma elongatum. The distribution of these taxa in the core indicated that the lake was initially shallow. The water level increased at the 240 cm horizon in the core, fluctuated in the subsequent sediment layers, and remained high above the 50 cm level, except for one possible short-term fluctuation, and increased to the present depth in the youngest sediments.

The fossil Chironomidae fauna of the Lake Grasmere core was analysed, and 35 taxa were recognised. Tanytarsini were the dominant component of the fauna with Corynocera sp. as the most abundant species during pre-Polynesian times (before ca. 1000 yr B.P.). During the Polynesian period Orthocladiinae sp. IX was dominant and in the youngest sediments, the European period, Chironomus became the dominant fossil chironomid. The abundance and composition of the fossil Chironomidae fluctuated markedly over the last 6000 years. These fluctuations could be partly correlated to changes in the stratigraphy of the sediments in the core. Layers of highly minerogenic sediment contained the lowest numbers of remains and fossil taxa, whereas high abundances and diversities were found in the sections of the core with higher proportions of organic matter. Some of the pronounced shifts in the structure of the Chironomidae community were caused mainly by changes in the hydrology and the inflows to the lake, and by variations in the rate and type of sedimentation. These variations induced alterations in the substrate type which appeared to have changed the dominance pattern of the fossil chironomid fauna. Changes in lake productivity influenced the composition of the fauna to a lesser extent.

In the fossil Cladocera fauna of the core, 14 species were distinguished. Two species were planktic and ten species belonged to the benthic Chydoridae. Several factors influenced the composition of the fossil Cladocera fauna, including increased input of minerogenous matter, changes in water depth, and lake productivity.

Concentrations of fossil pigments, chlorophyll derivatives, total carotenoids, and the ratio of chlorophyll derivatives to carotenoids exhibited frequent and distinct fluctuations during the past 6000 years of Lake Grasmere's history indicating alternating periods of low and higher lake productivity.

The recently deposited chironomid remains in surficial sediments from 32 lakes in the South Island were studied to establish relationships between faunal assemblages and limnological conditions of the lakes studied. A classification analysis based on the relative abundance of 19 chironomid taxa separated three main groupings of lakes and identified four lakes as outliers. These lake groups had distinctly different conditions which could be related to the composition of the chironomid fauna.

The stratigraphy of the fossil Chironomidae from Blue Lake, Mt. Kosciusko National Park, Australia, is presented for comparison. The fossil fauna comprised 28 taxa, but was dominated by Podonomus in the Late-Pleistocene sediments, by nr. Eukiefferiella in the early Holocene and by Chironomus in the younger sediments. Changes in temperature and substrate may have been mainly responsible for the changes in the composition of the fossil chironomid fauna during the last 13,000 years.

In correlating the stratigraphies of the different parameters studied in the Lake Grasmere core (organic matter content, Chironomidae, Cladocera, plant pigments) it can be shown that the lake has been influenced strongly by a geologically active and variable environment. Allochthonous minerogenous input was relatively high during the last 6000 years, but environmental disturbances of different degrees of magnitude caused pulses of increased amounts of mineral matter input. The response of the organic remains to these events was a decline in abundance and diversity. Two short periods (in the oldest and younger sediments) with higher lake productivity were indicated during which the lake was shallow and macrophytes were important. The longest stable period (from ca. 3000-1700 yr B.P.) was characterized by higher lake levels with a relatively great proportion of planktic diatoms and Cladocera. Lake waters were probably very clear and the sediments contained a large amount of benthic algae. The composition of the fauna in surficial sediments from several lakes could be used as analogues for fossil assemblages in the core. The fossil chironomid fauna from Lake Grasmere differed markedly from that in Blue Lake. Abrupt changes in the composition of the fauna and numbers of remains (as was found in Lake Grasmere) were restricted to the part of the Blue Lake core deposited during the late-Pleistocene, whereas changes in the fauna during the Holocene occurred gradually.

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CHAPTER I

GENERAL INTRODUCTION

Palaeolimnology, as defined by Delorme (1972), is the study of fresh waters of the past with special regard to lakes and ponds, the aim being to reconstruct the evolution of a lake and its drainage basin. Palaeolimnology deals with all physical, chemical, meteorological, and biological conditions pertaining to the lake during its developmental history. The sediments of lake systems provide a record of the processes which have operated within the terrestrial and aquatic ecosystems over space and time (Pennington, 1981). The data gained by analysing the sedimentary component of lake systems reveal information about the functioning and the dynamics of an ecosystem (Håkanson & Jansson, 1983). Sediments integrate the sum of the processes occurring during a lake's life-time and are frequently more representative of long-term equilibria than are modern water and biological samples. The latter may only represent the present state at the sample site due to the great temporal and spatial variations of water masses and biological assemblages in lakes (Binford et al., 1983; Longmore, 1986).

The study of sediments provides information about the effects of long-term or very slow processes occurring in the ecosystem, as well as sequences and rates of change in the evolution of a lake and its catchment. The understanding of these processes is an important requirement for the management of lake systems. Longmore (1986) suggested that sediment studies should be integrated more fully into the standard limnological monitoring programs, because palaeolimnological methods identify previous successive limnological conditions. In many parts of the world, anthropogenic impact on lake ecosystems has greatly altered their initial state and accelerated rates of change, often resulting in the degradation of the ecosystems involved (Schindler, 1985). Retrospective studies can be used to obtain baseline data on the pre-impact state of the system and to detect early responses of the lake system to perturbation (Davis, 1989). Studies of the sedimentary record might help to distinguish

between the effects of slowly increasing stress caused by human activities and deviations from natural background (Schindler, 1985). A further important aspect of palaeolimnological analysis is the opportunity it represents for studying the effects of rare events on ecosystems. Environmental disturbances which occur once per century or less are only encountered by chance during the course of modern ecological studies. Examples of rare events include wild fires, floods, droughts, high intensity windstorms, and earthquakes. The long time series available in the fossil record of lake sediments are potentially useful as they allow analysis of the response of lakes to such events (Davis, 1989).

Sediments can be analysed for a wide range of physical, chemical, and biological variables. The aim of palaeolimnological study is to detect patterns in the data which can then be interpreted in terms of past conditions of the lake (Birks, 1986). This thesis was designed as a multiparameter study of fossil Chironomidae, Cladocera, and pigments from a sediment core from Lake Grasmere, Canterbury. The multidisciplinary approach is advantageous for several reasons. Possessing different data for the same sediment profile provides the means of testing the accuracy of palaeoecological interpretations - only those which fit all data sets can be true (Pennington, 1981). Additionally, it widens the scope of those interpretations as the species composition and abundance of the different animal groups are not controlled by the same set of environmental factors (Crisman, 1988). Therefore, individual biotic elements may be used as indicators for different controlling factors in lake systems.

The main emphasis of the present study is the analysis of fossil Chironomidae. Besides the description of the fossil chironomid stratigraphy from Lake Grasmere, the results of an analysis of fossil Chironomidae from Blue Lake, Australia, are included in this thesis as a comparative study. The fossil record from Blue Lake covers the period of the Late-Pleistocene and Holocene, thus giving information about the fossil chironomid fauna during the important dynamic environmental changes occurring at the end of the Pleistocene and the beginning of the Holocene (Veevers, 1984). To facilitate the interpretation of chironomid associations in the past of Lake Grasmere, chironomid remains from present day surficial sediments of a

number of lakes in the South Island have been examined. The recent chironomid assemblages have been analysed with regard to the different limnological conditions of these lakes to help interpretation from the fossil associations.

1.1. Family Chironomidae

Chironomidae (Class: Insecta, Order: Diptera) are a large family (ca. 5000 described species) of non-biting midges which are prominent as larvae in virtually every type of aquatic habitat. They are the most widely distributed and frequently the most abundant group of insects in fresh water environments (Pinder, 1986). Chironomids have four life-history stages, egg, larva, pupa, and adult, of which the larval stage consists of four instars and is the longest (Oliver, 1971).

Because of the wide ecological range of the group and the sensitivity of certain chironomid species to environmental conditions, members of this family have been used successfully as indicators of changes in aquatic environments (Frank, 1983; Wiederholm, 1980; Gerstmeier, 1989). The composition and relative abundance of the larval chironomid fauna change in response to oxygen supply, food availability, temperature and sedimentation regime (Warwick, 1980).

Chironomid communities are also influenced by factors such as food quality and quantity, nature of the substratum, and water depth (Pinder, 1986). Water quality, as indicated by parameters such as the pH, salinity, oxygen concentration, temperature, and the degree of pollution, strongly influences the composition of the chironomid fauna. Most species are adapted only to a certain range of these parameters and a marked increase of, for example, pH or salinity usually results in a decrease in species numbers. In the case of heavy metal pollution, larvae show characteristic deformities of the mouth parts (Pettigrove, 1989; Warwick, 1988).

The specific differences of chironomids in their tolerance of low oxygen concentrations were used in earlier studies to classify the trophic state of lakes in Europe and North America. Thienemann's (1920, 1928) studies of profundal chironomids from German lakes linked

together the composition of the profundal chironomid assemblages and the trophic state of lakes as a function of the oxygen concentration of the hypolimnion. Brundin (1951) refined this lake typology, and Sæther (1975) expanded the European classification to include North American chironomid species. In the latest midge typology, profundal as well as littoral and sublittoral, chironomid species of Nearctic and Palearctic lakes form 15 chironomid communities characteristic of 15 trophic levels ranging from ultra-oligotrophic to strongly eutrophic (Sæther, 1979).

Studies by Sæther (1975) demonstrated that there are highly significant correlations between chironomid associations and the ratio of chlorophyll a : mean depth and total phosphorus : mean depth. These findings were corroborated by Wiederholm (1980), who developed a Benthic Quality Index based on certain chironomid species. Brundin (1956a, 1965) predicted that the lake-type system based on chironomid communities as indicators of trophic state would have worldwide validity. To date neither the chironomid research in Australia nor that in New Zealand has produced evidence to verify this prediction for these regions.

1.2. Chironomidae in Palaeolimnological Research

Chironomid larvae possess chitinous head capsules which are shed four times with the exoskeletal integument during larval growth. These head capsules are usually abundant and well preserved in lacustrine sediments and retain distinct morphological features facilitating the identification of the chironomid taxa. They therefore fulfil the prerequisites of suitability for palaeoecological research.

The fossil chironomid remains of lake sediments can be used to follow the development of certain taxa through time and to indicate former environmental conditions at the time of sedimentation (Stahl, 1969; Frey, 1976; Hofmann, 1986a; Walker, 1987). Several studies have demonstrated that changes in the composition of the fossil chironomid communities indicated variations in climatic conditions and trophic levels (Hofmann 1971a, 1978; Walker & Mathewes, 1987a,b, 1989b,c; Walker et al., 1991a,b) or anthropogenic influences on the lake and

its catchment (see Mannion, 1989). Furthermore, fossil chironomids have provided information regarding acidification trends (Henriksen et al., 1982) and salinity fluctuations (Clair & Paterson, 1976). Studying fossil chironomids is not only of importance for the description and elucidation of the developmental history of lakes but it also provides an opportunity for long-term observation of populations and community succession, as well as the dispersal of species. This aspect is particularly relevant to my study because the knowledge of community structures and ecology of the New Zealand Chironomidae is far from being complete (Cranston & Martin, 1989).

Cores for studying fossil chironomids should be taken from the deepest part of the lake basin because the profundal chironomid communities indicate the conditions of the whole lake whereas the sublittoral and littoral chironomids possibly only reveal information about the part of the lake in which they lived (Brodin, 1982; Frey, 1988; Hofmann, 1983b, 1988). The sedimentation site of remains, the thanatotop according to Böger (1970), does not always represent the habitat of the live organism. Profundal sediments may contain remains of littoral species which have been moved offshore before deposition. Hofmann (1971a) and Schakau and Frank (1984) found relatively high percentages of littoral species in deep-water sediments of Schöhsee and Lake Tegel respectively. Iovino (1975) and Walker et al. (1984) carried out a comparison of living associations of Chironomidae and fossil chironomid assemblages from sediments in several lakes and their results indicated a good correlation between the composition of the living chironomid communities and fossil assemblages at the different sampling sites studied.

The number of head capsules recovered from sediments is usually smaller than that expected from the size of the chironomid populations present. A partial explanation is that the first- and second instar larvae of some species completely dissolve the chitinous proticle of the head capsule before moulting, whereas third-and fourth instar larvae retain at least part of it. Consequently, remains of the first two instars are rarely found (Iovino, 1975). Fourth instar remains of certain taxa may also be blown ashore still attached to pupal exuviae resulting in an underrepresentation of fourth instar head capsules of these taxa in the sediments (Hofmann, 1971a). Other explanations for

the numerical difference between fossil assemblage and the population that produced them, may be postmortem redeposition and differential preservation. Because there is little knowledge about these processes, it is as yet not possible to undertake quantitative reconstruction of past chironomid populations (Crisman, 1988).

1.3. Fossil Chironomid Research in Australasia

In North America and Europe, analyses of fossil chironomids are common (see Hofmann 1986, 1988; Walker 1987). In the Southern Hemisphere however, few studies exist. In Australia, Paterson and Walker (1974) studied the fossil chironomid fauna of a saline lake, Lake Werowrap. They showed that salinity and competition may significantly affect the distribution of Tanytarsus barbitarsus. They suggested that the restriction of T. barbitarsus to highly saline waters may not be the result of its inability to tolerate waters of reduced salinity but due to competition from other tube-building, sediment-feeding chironomids, e.g. Chironomus duplex, in waters of lower salinity.

In New Zealand, Boubee (1983) studied the developmental history of Lake Maratoto (Waikato) using chironomid remains. The results of his study showed a succession of the fossil chironomid fauna as a response to changes in the typological development of the lake which correlated well with data derived from pollen and chemical analyses (cf. Lowe & Green, 1987). Deevey (1955) analysed a short core from the Pyramid Valley upper swamp deposit but did not include a detailed chironomid analysis. The most abundant head capsules in the Pyramid Valley sediments belonged to Dryadotanytarsus duffi (description by Deevey) which was later recognized as belonging to the genus Corynocera (Hirvenoja, 1961). Head capsules of this species were also among the most abundant in the sediments of Lake Grasmere and common in the sediments of Lake Taylor in a study of short cores from these lakes (Schakau, 1986).

1.4. The Present Study

The aim of the present work was to describe the fossil chironomid fauna from a sediment core from Lake Grasmere and to gain information about some aspects of the ecology and dispersal of New Zealand chironomid taxa in space and time. With regard to the developmental history of Lake Grasmere, an attempt was made to relate the occurrence of certain fossil species and changes in the composition of the fauna to variations in the past limnology of the lake or to changes in climatic conditions. Chironomid analysis has to be considered as only one aspect of sediment analysis. Therefore, the results of this study were compared with information derived by supplementary methods. These included the analysis of fossil Cladocera and fossil pigments from the same core, and an investigation of chironomid assemblages from surface sediments collected from thirty-two lakes in the South Island.

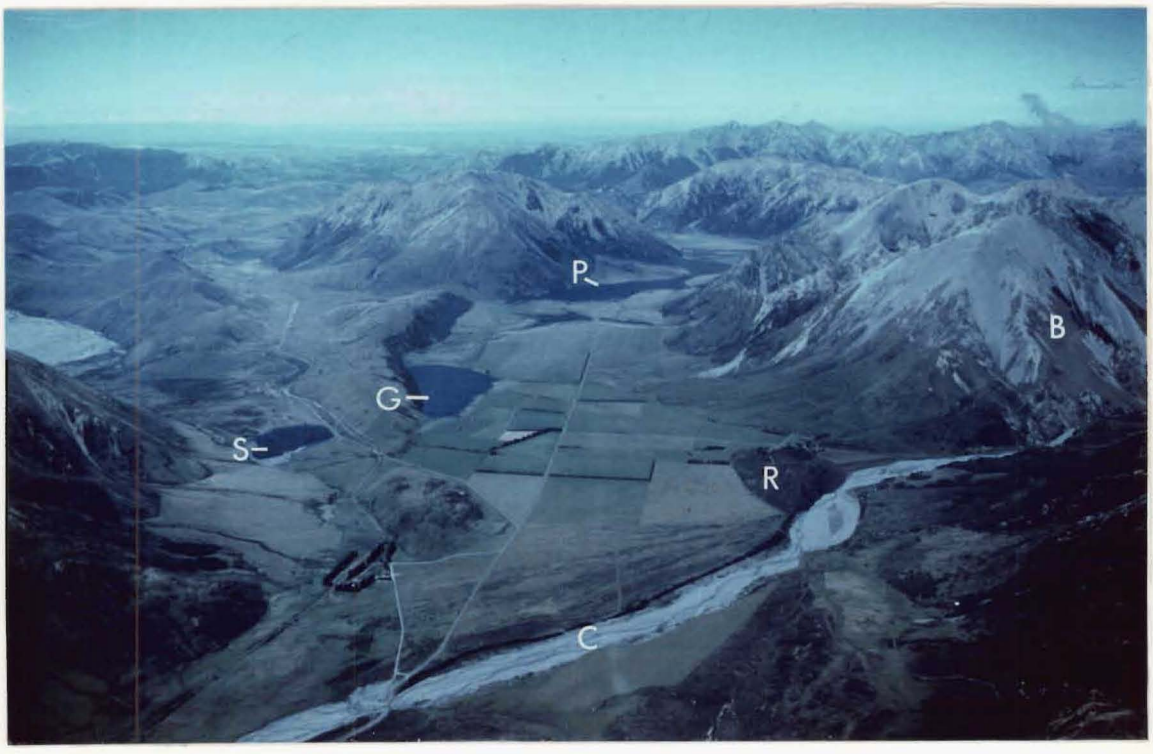


Plate 2.1. Aerial photograph of Lake Grasmere (G) and its catchment, view towards south east. Lake Pearson (P) is visible in the background, Lake Sarah (S) is located to the left of Lake Grasmere and the shingle river in the foreground is the Cass River (C). The mountain to the right is Little Bailey (B) and the hill in front of Little Bailey is Romulus (R) (Photo: Janet Wilmshurst).

CHAPTER II

METHODS

A sediment core was obtained from Lake Grasmere (Plate 2.1.) in mid-February 1988, using a hand-operated modified Livingstone corer (Green, 1979; Green & Lowe, 1985) operated from a boat. The coring site was located in the southeastern part of the lake at a water depth of 10.5 m (Fig. 2.1.). The coring tube was a 5 m long PVC pipe with a diameter of 50 mm. For the coring procedure, the corer was used as an open drive sampler (Aaby & Diggerfeldt, 1986) omitting the piston which did not show any positive effect on the coring. The sediment of Lake Grasmere consists to a high degree of minerogenic matter. Therefore, the coring tube could be pushed manually into the sediment only for the first 1 m. Thereafter, a hammer was used to force the tube into the sediment to the final depth. 326 cm of sediment were recovered in the core from the lake. The bottom 6 cm of the core was composed of medium grey clay and silt. This layer prevented further penetration of the coring tube. On return to the laboratory, the core was cut in half longitudinally. One half of the core was stored undisturbed for reference in the Zoology Department, University of Canterbury. For storage, the reference core was wrapped in aluminium foil and sealed in a plastic envelope. The second half of the core was used for the study of microfossils, fossil pigments, and analyses of the sediments.

2.1. Sediment Analyses

Before the subsampling of the sediment core was carried out, the sediment layers were photographed (Plate I in Appendix I) and described. The characterization of the sediments included a colour description using the standard Munsell charts and an analysis of the deposit elements of the core (Aaby & Berglund, 1986). Deposit elements of sediments are divided into five main groups: Turfa, Detritus, Limus, Argilla, and Grana according to Troels-Smith (1955) (see Aaby & Berglund, 1986, p. 234). The proportion of elements is estimated on

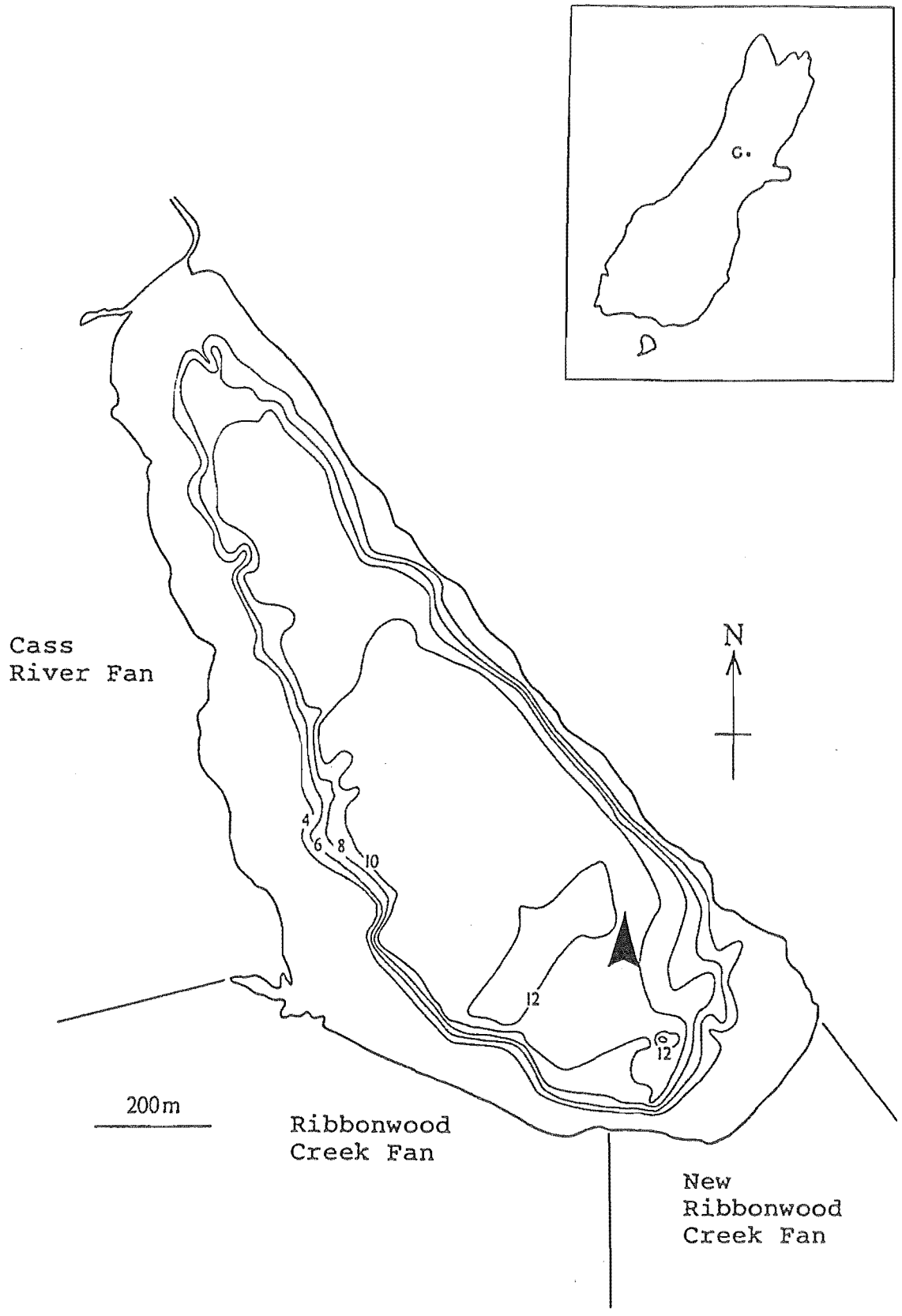


Fig. 2.1. Bathymetric map of Lake Grasmere (Contour Interval: 2m). The black triangle indicates the sampling site of the sediment core. The inset shows the South Island of New Zealand with the location of the lake studied (G).

the 5-class scale (0-4) implying that the total of deposit elements must always be four. The presence of traces of a given element is indicated by using the plus sign (+). For the analysis, a water suspension of a small quantity of sediment was made on a glass slide and examined under the light microscope at x150 magnification. The relative abundance of the elements present is given in Fig. 3.2.

After completion of the sediment description, subsampling of the core was undertaken. For the analysis of sedimentary plant pigments 2 cm^3 cubes of sediment (28 samples), mostly at 10 cm intervals throughout the length of the core, were sectioned off by using a razor blade, then wrapped in plastic and aluminium foil, and immediately frozen for storage at -18°C (Sanger & Gorham, 1972). Samples for water and organic content, and parallel samples for the microfossil analyses, consisted of 1 ml of wet sediment. The sampling was carried out with an open-cut, 5 ml volume, plastic syringe at intervals usually of 10 cm. The frequency of sampling was increased in sections of the core where stratigraphic changes were visible. Care was taken not to include any of the smeared surface of the section. Water content was measured immediately after sampling by determining the weight loss of the sediment at 70°C after 24 hours. The organic content was expressed as loss-on-ignition, which was measured after ashing the dry sediment at 550°C for two hours. A determination of the carbonate content was carried out on 17 samples by ashing the sediment for four hours at 945°C. The carbonate contents of these samples were less than 1% of the dry weight, and the remaining samples were not tested for carbonate. Determination of loss-on-ignition was also carried out on parallel samples to those used for sedimentary pigment analysis.

2.2. Microfossil Analyses

Two methods were employed to prepare sediment samples for the microfossil analyses.

A preliminary study of fossil Chironomidae included 18 samples taken at the following levels in the core: 3, 6, 14, 23, 30, 55, 90, 130, 155, 190, 210, 235, 260, 290, 310, 315, 317, and 326 cm. These samples were treated as described by Hofmann (1971a) and Walker (1987). For

deflocculation, 1 ml of wet sediment was mixed in a 50 ml Erlenmeyer flask with hot 10% potassium hydroxide solution on a magnetic stirrer for 45 minutes and then rinsed in a 100 μm sieve with copious amounts of water. If carbonates were present in the sediment, the samples were treated with 10% hydrochloric acid and again sieved and rinsed. Subsequently, the remains were transferred to a centrifuge tube using minimal amounts of water. Small quantities of the wet residues were transferred to a sorting microscope slide with grid lines for orientation and examined under a stereo microscope with a magnification of 65x. Each head capsule was picked out using a fine brush and mounted directly in polyvinyl lactophenol with the ventral side upwards. The chironomid remains of the entire sample were retrieved to determine absolute numbers of fossils. This method was employed in the preliminary study as the placement of single head capsules under coverslips provided more suitable material for identification and microphotography of the fossil Chironomidae taxa than the quantitative slides.

Quantitative slides of the remaining 38 sediment samples were prepared according to a slightly modified method described by Boubee (1983) and Frey (1986). In order to economize on sediment material and work, the samples were used for both chironomid and cladoceran analyses by using differently diluted fractions of the same sample.

As for the chironomid analysis, the cladoceran analysis required estimates of the number of remains per ml of sediment for each species present at each stratigraphic level studied. These estimates were based on microscope slide preparations, with each coverslip representing a known fraction of the processed sample. Each coverslip analysed thus provided a separate determination of the fossil densities of the individual taxa. Usually, sediment samples contain far more fossil Cladocera exuviae than fossil chironomid head capsules, making it unnecessary to sort the residues of the entire sample. A higher dilution of the sediment residues was thus used for the preparation of 10 "Cladocera slides" from each sample. The estimate of remains per ml of sediment was based on this aliquot fraction.

The remaining sample was concentrated and transferred to microscope slides and mounted. For the chironomid analysis, all slides prepared from 1 ml of sediment were scanned for head capsules. The same slides were also used for the Cladocera analysis, if the 10 "Cladocera slides" did not contain a sufficient number of remains (see Appendix, Table III.4.). Frey (1986) recommended that when counting fossil Cladocera, at least 200 usable exuviae should be included in the analysis. This number was achieved as far as possible.

The preparation of quantitative slides was undertaken as follows: 1 ml of wet sediment was heated in 20 ml of 10% potassium hydroxide solution in a 50 ml Erlenmeyer flask with stirring for 30 minutes to disintegrate the sediment. This was then sieved through a 40 µm screen, rinsed with water and transferred back to the Erlenmeyer flask. To dissolve mineral matter in the sample, an equal volume of 20% hydrofluoric acid was added and the solution was allowed to stand overnight. 10% hydrochloric acid was added and the mixture was sieved and rinsed using a 40 µm sieve, before being transferred back to the Erlenmeyer flask. Five drops of Chlorazol Black solution and 5 ml of 50% ethanol were added to dye the chitinous remains. After 24 hours, the remains were sieved and rinsed again in a 40 µm sieve, and transferred to a glass centrifuge tube. Water was added to a final volume of 5 ml. Keeping the material homogeneous, 40 µl aliquots of the sample were removed individually with a Brand positive displacement micropipette. This pipette was used with plastic capillaries which possess an aperture large enough to accomodate the largest cladoceran remains. The aliquots (2 samples per slide) were transferred to microscope slides, and heated slightly on an electric thermal plate to evaporate excess water in the sample. Subsequently, the remains were mounted in 0.04 ml glycerin jelly under square 22 mm coverslips. The last procedures were repeated until 10 slides were processed. These slides were used for the Cladocera analysis. The solutions containing the remaining part of the sediment residues were left standing for several days to allow the lighter remains to settle. The overlying water (up to 1-2 ml) was then removed, the volume depending on the amount of sediment left. The decanted water was examined under a microscope to ensure that no remains were lost. Aliquots of 0.04 ml were mounted on slides as described above until all residues of each sample were mounted. The recognizable

microfosssils on the quantitative slides were counted under a microscope with a magnification of 100x.

For the chironomid analysis, all remains were counted to determine the absolute number of fossil Chironomimidae in 1 ml of sediment. Every chironomid fragment was counted as a whole animal with the exception of head capsules which consisted of less than one half of the mentum. These fragments were excluded. This method of counting ignored possible accumulation of remains shed by the same individual over several instars. The possibility of lesser occurence of remains shed by taxa with a larval life cycle longer than one year, or the more frequent remains of multivoltine taxa was not included in the analysis.

The identification of the fossil chironomid head capsules was carried out with reference mainly to the New Zealand identification keys of Forsyth (1971) and Stark (1989). Several overseas keys were also referred to including: Pankrovata, 1970; Hofmann, 1971b; Mason, 1973; Martin, 1974, 1975; Oliver et al., 1978; Cranston, 1982; Simpson & Bode, 1980; Wiederholm, 1983.

The results of the fossil counts are presented as the relative abundance of chironomid taxa in the samples. Influx rates for each taxon could not be given because accurate measures of the sedimentation rate for Lake Grasmere were not available.

2.3. Data Analyses

Analysis of the results was based on the above mentioned percentage data of each taxon in the sediment samples. Multivariate analytical methods were used to investigate patterns in community structure of fossil Chironomidae and Cladocera.

A comparative community similarity index, the percentage similarity of community (PSC) (Renkonen, 1938; Whittaker & Fairbanks, 1958; Stark, 1985) was used as a basis for a cluster analysis. This index incorporates quantitative information on species occurrence and is given by the formula

$$PSC = 100 - 0.5 \sum (a-b) = \sum \min (a-b)$$

where a and b are, for each species, the respective percentages of the total fossil remains in sample A and B. PSC was used here as a dissimilarity index (1-PSC) to make comparisons of community similarity for the faunal compositions during successive time periods (core samples), or for the chironomid fauna of selected South Island lakes, on a scale of increasing dissimilarity from 0.0 to 1.0.

The dissimilarity matrices formed from site/taxa group analyses are presented graphically as dendrograms. The dendrograms were produced using average linkage clustering (Clifford & Stephenson, 1975; Stark, 1985). This technique joins two groups of samples together at the average level of similarity between all members of one group and all members of the other. The aim of classification or cluster analysis is the assignation of objects, in this case samples/taxa, to groups in such a way that each group reveals some distinct characteristic of the sample (Orloci, 1978). One disadvantage of classification is that it always produces discrete groupings, even when there is no meaningful ecological pattern in the data. As a means of confirmation of groupings derived from the cluster analysis, an ordination analysis was performed on the data sets. The ordination technique chosen was a reciprocal ordering or averaging (Hill, 1973). In contrast to cluster analysis, ordination methods attempt to represent the relationships between the sample units in a continuum of one or more dimensions. In reciprocal ordering, the objective is to arrange taxa and sample units

into an order that maximises some measure of correlation. The ordering may use species scores for samples or sample scores for species such that the species scores correspond to points of optimal response on an environmental gradient and the sample scores represent co-ordinates on extracted axes identified as the canonical variates of a certain type of scalar product matrix (Orloci, 1978). Results (sample scores) are presented as scatter diagrams in which the distances between the individual sample units represent their relative similarity. The axes are described by a hypothetical environmental gradient (ter Braak & Prentice, 1988). In palaeolimnologtive similaritythe type of environmental gradient responsible has to be inferred from the resulting pattern based on the faunal distribution.

The analyses were run on a Personal Computer using slightly modified versions of programs given in Orloci (1978): RQT.BAS for ordination, and ALC.BAS for average linkage clustering (Stark, pers. com.).

CHAPTER III

DESCRIPTION OF THE STUDY AREA AND SEDIMENT RECORD

3.1. Location and Formation of Lake Grasmere

Lake Grasmere is located in the Cass Basin in the montane region of the Waimakariri River catchment, Canterbury (Plate 2.1.). The Waimakariri River drains a section of the Southern Alps and the topography of its catchment is heavily modified by glacial and subsequent post-glacial erosion (Hayward, 1967).

The choice of Lake Grasmere as the study site was influenced by the existence of earlier studies dealing with the glacial geology (Gage, 1977), geomorphology (Soons, 1977), history of the vegetation of the Cass area (Moar, 1971; Moar & Lintott, 1977), and the limnology of the seven lakes in this region (Stout, 1969). Furthermore, the benthic and macrophyte-associated fauna of Lake Grasmere is well known (Stark, 1981; Timms, 1982, 1983).

Lake Grasmere (43°0.5′ South, 171°45′) is a small, shallow lake, situated at about 583 m above sea level (Irvin, 1975). The lake has an area of 0.67 km^2, a maximum depth of 15 m and a mean depth of 7.8 m (Fig. 2.1.). There is one surface inlet stream and, in addition, the waters of the Ribbonwood Creek reach the lake as springs after flowing underground through the New Ribbonwood Creek Fan. The outlet is Grasmere Stream situated at the northern end of the lake which flows into the Cass River. The catchment area is predominantly tussock grassland, 50% of which is used for agriculture. Along the eastern side of Lake Grasmere, Nothofagus solandrii (Mountain Beech) extends to the margin of the lake.

Lake Grasmere (Fig. 2.1.) was formed partly by glacial activity, and partly by alluvial aggradation (Gage, 1959). The last glaciation in New Zealand, the Otira glaciation (ca. 75,000 - 14,000 yr before present (B.P.)) had three advances in the Waimakariri catchment (Burrows, 1978; Suggate, 1990). During the last phase, the Poulter advance, a lobe of the Waimakariri Glacier entered the Cass Basin,

branching into two main lobes at the sites of the modern Lakes Grasmere and Sarah (Fig. 3.1.). The ice withdrew possibly about 13,500 years ago and Lake Grasmere originated after the ice retreat (Gage, 1959). The lake is partly dammed by ice-eroded rock. The greater part of the lake perimeter is formed by three extensive alluvial fans (Fig. 2.1.). The ages of the Cass fan and the Old Ribbonwood fan are uncertain but both fans have not grown for at least several hundred years (Soons, 1977). Deposition has continued in the New Ribbonwood fan in historic times decreasing the area of the lake. Originally, the lake probably extended eastwards as far as the end-moraine loop deposited during the Poulter advance (Gage, 1959). It is possible that the Old Ribbonwood Creek fan began growing before or simultaneously with the Poulter advance. Its formation continued after the retreat of the ice which is shown by the way that the Ribbonwood fan overtopped the Poulter end-moraine (Soons, 1977). The Cass fan could only have been deposited after the basin had become largely, if not entirely, ice-free. Old stream channels on the surface of the Cass fan show that the river has migrated in the past across the floor of the Cass Basin, depositing material in an arc which extends from Lake Grasmere on the south-east to Waterfall Terrace on the west (Burrows, 1983). The eastern two-thirds of the fan were formed when the Cass River flowed south of Romulus Hill. During more recent times, the river has been confined to the western side of its fan and has been relatively stable with little deposition (Burrows, 1983).

3.2. Vegetation History and Past Climate

The late glacial period began about 14,000 years ago with rapid ice retreat from the positions held during the glacial maximum (Burrows, 1984). The development of vegetation after the end of the Otira glaciation in the South Island followed a general pattern from open grassland-shrubland through shrubland to forest. The successional changes of the vegetation were not synchronous in different areas of the South Island (Moar, 1971).

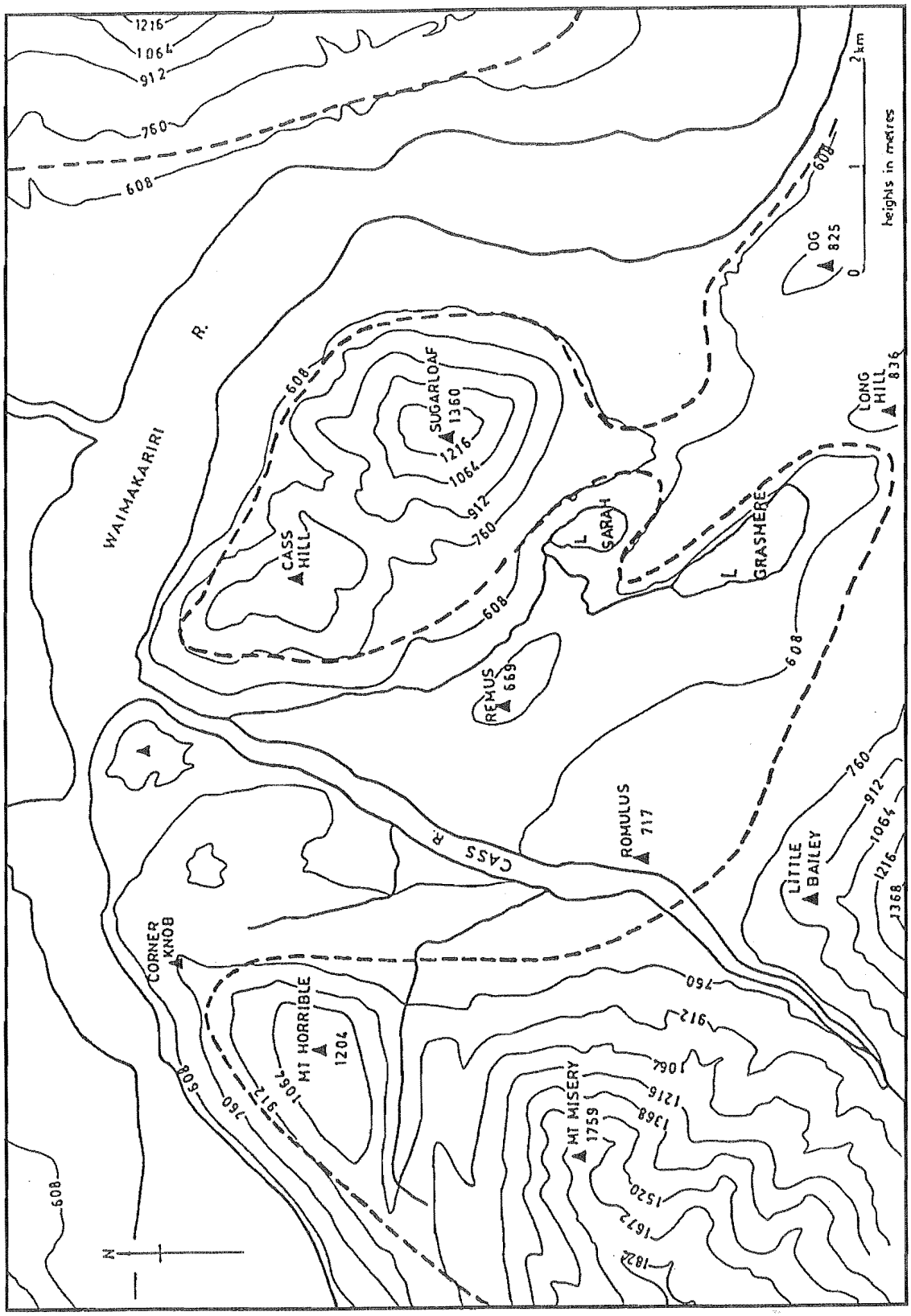


Fig. 3.1. Map of the Cass Region. The broken line marks the approximate ice-limit near the end of the Poulter Advance (modified from Lintott & Burrows, 1973).

In a pollen diagram from Kettlehole Bog, near Lake Grasmere, six pollen zones were recognized (Lintott & Burrows, 1973). During the late glacial period, vegetation changed from herbaceous plants (Zone 1) to a predominance of Coprosma and then Halocarpus pollen (Zone 2) indicating a slight warming of the climate. The rapid climatic amelioration at the beginning of the Holocene, 10,000 yr B.P. (McGlone, 1988) caused the spread of forest consisting of podocarps, including the species Prumnopitys ferruginea, Dacrycarpus dacrydioides, and Prumnopitys taxifolia (Zone 3 and 4). The climate during Zone 4 was at a peak of mild temperatures and reliability of precipitation. Mean annual temperatures might not have been much higher than at present, but the extreme range was probably less. The present climate at Cass does not allow the growth of Prumnopitys and Dacrycarpus. Podocarp forest remained dominant in the area until at least 7500 yr B.P. (Moar, 1971). Pollen of the Nothofagus fusca group became dominant in Zone 5 indicating a near total replacement of tall podocarp forest by Nothofagus fusca and N. solandri. This transition may represent a change in climate from mild temperatures and high reliable rainfall, to lower minimum temperatures, greater temperature extremes, lower rainfall and the occurrence of periodic drought characteristic of the present climate (Burrows, 1979).

In the last pollen zone from Kettlehole Bog, Zone 6, Nothofagus pollen decreased whereas Gramineae and Cyperaceae pollen increased indicating widespread clearance of forest by fire and its replacement with the present vegetation pattern. The most likely cause of the fires is thought to be burning by Polynesian hunters. Polynesian people settled in New Zealand about 1200 yr B.P. (Davidson, 1984), and the fires, which were probably caused by the Polynesians, occurred between 500 and 1000 years ago (McGlone, 1988, 1989). Additional burning occurred after 1857 when the first Europeans settled in the Cass district and used fire to clear land for sheep grazing (McLeod & Burrows, 1977).

Fire also had an effect on the Cass environment before human settlement. Natural fires caused by lightning have occurred in the area at intervals since deglaciation as shown by the dated charcoal layers found in different locations at Cass (Molloy, 1977).

3.3. The Present Climate at Cass

The climate of the Cass area is typical of an intermontane basin and is characterized by high mean and maximum temperatures in the summer months, and winters which are relatively mild through moderation by north-westerly winds. Mean monthly air temperatures recorded at the Cass Field Station from 1961 to 1964 were 1.6°C in July and 15.7°C in February with a mean annual air temperature for the same period of 9°C (Greenland, 1977).

Cass is located within the rain shadow of the Main Divide (Sturman, 1986). West to north-west airflows predominate and bring rain. There is a steep rainfall gradient with high values in the west and low values in the east. The Cass area lies on the 1,250 mm mean annual isohyet (Greenland, 1977). Maximum precipitation occurs in spring and the driest months are February and March (Ryan, 1987). Monthly variation in precipitation is small, ranging from a mean of 89 mm in February to 130 mm in October at the Cass Field Station. Snow may fall in the Cass Basin on a few occasions in winter, but seldom persists for any length of time.

The Cass region and Lake Grasmere have a windy climate, with a reported average annual wind speed of 4.9 m/sec (from data measured for two years at the Cass Field Station (Greenland, 1977). Observations on wind directions at the Cass Field Station showed that northwesterly winds occurred 51% of the time. Only 20% of the observations indicated calm conditions, and even this might be an over-estimate since most observations were taken in the mornings, which are normally calmer than later times in the day. Percentage frequencies of wind directions were for from southeast to northwest, and 13% from south to southwest. Further details on the climate of the Cass area is given by Greenland (1977).

3.4. Limnology of Lake Grasmere

3.4.1. Physical Features

Thermal stratification seldom develops in Lake Grasmere because of the shallowness of the lake, and its exposure to the prevailing northwesterly winds. The maximum surface water temperature was 21°C in summer, and the minimum winter temperature was 0°C (Stout, 1975a); and ice may form over all or part of the lake in winter. Light penetration, measured using a Secchi disc, is variable. Extremes of 0.42 m (September, 1970 following heavy rains) and 8.2 m (May, 1970) have been recorded (Stout, 1972, 1977). Fluctuations are related to silt loads or plankton densities.

3.4.2. Chemical and Biological Features

The trophic status of Lake Grasmere was assessed as mesotrophic on the basis of phytoplankton community structure (Flint, 1975), plankton and water chemistry (Stout, 1969, 1975b, 1977), and heterotrophic potential (Spencer, 1978). The most recent assessment of the trophic status of the lake was undertaken by Sanoamuang (1992) based on her study of rotifers from Lake Grasmere. According to the species composition and the measured densities of rotifers, the lake is now considered to be eutrophic. Maximum densities of rotifers have increased from 300 individuals/litre in October 1969 (Stout, 1984) to 1600 ind/l in May 1989 and to 1500 ind/l in October 1989 (Sanoamuang, 1992). Pomphylox sulcata (Hudson), one of the dominant rotifer species recorded from Lake Grasmere, is an indicator species for eutrophic conditions in lakes (Sanoamuang, 1992).

The frequent mixing of the lake water and extensive macrophyte beds ensure that the lake water is usually well oxygenated at all depths. However, a low oxygen concentration (36% oxygen saturation of the bottom waters) was recorded following a few days of exceptional summer calm with thermal stratification (Stout, 1977). The pH of the lake water is normally close to neutral. During algal blooms, which may occur in February or March, the pH may rise to 8.3 (Stout, 1977). A high concentration of silica in the lake waters derived from the

greywacke bedrock in the drainage area, contributes to the relatively high abundance of diatoms (Stout, 1972). Stout (1984) reported a conductivity value of 89 µmhos/cm in Lake Grasmere.

The phytoplankton is dominated by the diatoms, Cyclotella stelligera, Asterionella formosa, and Diatoma elongatum (Stout, 1984). Filamentous and colonial green algae may also occur (Stout, 1972, 1977). Values for phytoplankton chlorophyll a have been recorded with a maximum of 7.9 mg/m^3 (Stout, 1984). Lowest values usually occur in May and June (Stout, 1972). The most abundant taxa of the zooplankton are the cladocerans, Ceriodaphnia dubia and Bosmina meridionalis (Stout, 1991). Also several species of rotifers occur, the most common being Polyarthra cf. dolichoptera, Keratella cochlearis, and Pompholyx sulcata (Sanoamuang & Stout, in press).

Lake Grasmere contains several species of fish, including brown trout (Salmo trutta), rainbow trout (Oncorhynchus mykiss), long-finned eel (Anguilla dieffenbachii), upland bullies (Gobiomorphus breviceps), and Koaro (Galaxias brevipinnis) (Stout, 1975).

Elodea canadensis is the most abundant macrophyte in Lake Grasmere forming extensive beds in water from 0.5 to 7-8 metres deep. Isoetes alpinus is found in shallow water on the eastern shore and Chara sp., Nitella sp., Myriophyllum propinquum, Ranunculus fluitans, and Potamogeton cheesemanii are also present in the lake (Stark, 1981).

The present chironomid fauna in Lake Grasmere is composed of 17 species (the highest number recorded from any New Zealand lake) belonging to five subfamilies (Stark, 1981). The chironomid fauna found in the macrophyte zone was more diverse than that of the benthos, and nearly all species found in the bottom mud were present also amongst aquatic plants (Stark, 1981). The exception was Cladopelma curtivalva which occurred only in benthic samples (Timms, 1983). Although only four chironomid species were found in the benthos, two of these, Chironomus zealandicus and Macropelopia spp., contributed considerably to the relatively high benthic standing crop in Lake Grasmere. The remaining benthic chironomids were Chironomus sp.a and Cladopelma curtivalva (Timms, 1983).

Fig. 3.2. Lake Grasmere: Stratigraphy of the core with a colour description and deposit element analysis of the sediments.
Abbreviations used: Dg - Detritus granosus,
Ld - Limus detrituosus, Lso - Limus siliceus organogenes,
As - Argilla steatodes, Ag - Argilla granosa,
Gmin - Grana minora.
Lithological symbols: ▤ - Clay/Silt, □ - Clay Gyttja,
▮ - Organic content >10%, ▦ - Grana minora.

3.5. Core Description

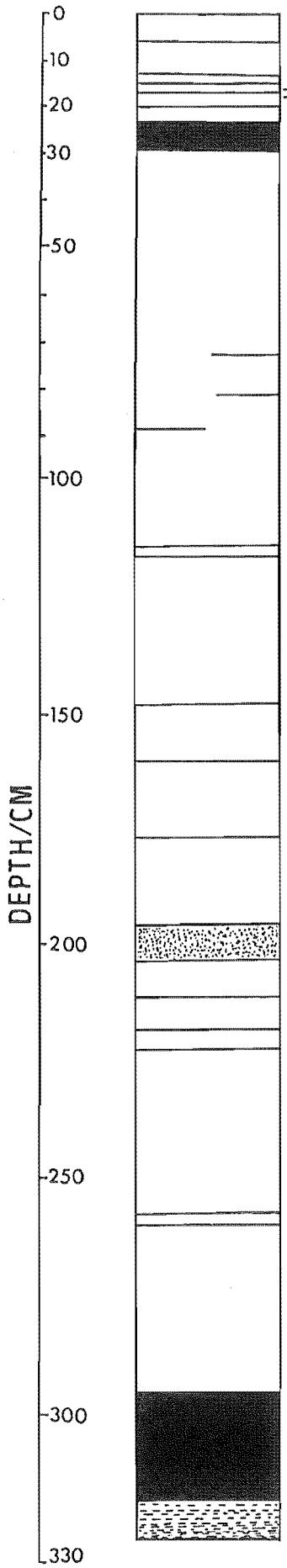
In the core obtained from Lake Grasmere, 326 cm of sediment were recovered. A stratigraphy of the core with a colour description of the sediment layers and the results of the deposit element analysis are presented in Fig. 3.2. The sediments of the core consisted mainly of clay gyttja which exhibited lithographically recognisable layers of varying shades of olive grey. Three dark zones occurred between 29-23 cm, 204-196 cm, and 319-295 cm. The 204-196 cm layer was a dark greenish grey. A medium dark grey lamination was visible between 260 cm and 258 cm. Layers which appeared very light in comparison with the other sediments of the core were found at the bottom of the core (326-320 cm, medium grey), and a thin light grey layer which was visible in the younger sediments (15-13.5 cm). The stratigraphy of the sediment layers above the 23 cm horizon showed five relatively thin layers of different colours indicating a highly variable sedimentation regime.

3.5.1. Sediment Composition

The analysis of the deposit elements in the core showed that the sediments consisted of six elements. The definitions of the deposit elements are according to Aaby and Berglund (1986).
The inorganic fraction was composed of:
Argilla steatodes, particles of clay ≤ 0.002 mm (As);
Argilla granosa, particles of silt 0.06 - 0.002 mm (Ag);
Grana minora, particles of sand 2 - 0.06 mm (G min).
The organic fraction was composed of:
Detritus granosus, fragments of ligneous and herbaceous plants, and animal fossils (except molluscs) ≤ 2 mm ≥ ca. 0.1 mm (Dg);
Limus detrituosus, fragments of plants and animals (except siliceous skeletons) ≤ 0.1 mm, +/- humous substance (Ld);
Limus siliceus organogenes, diatoms, siliceous skeletons of organic origin, or parts of these, particles ≤ 0.1 mm (Lso).

The bottom layer of the core (326-320 cm) appeared to be composed entirely of A. steatodes and A. granosus. The sediments above that layer between 318 and 295 cm contained L. detrituosus and a small amount of L. siliceous organogenes besides the clay and silt fraction

LAKE GRASMERE CORE



COLOUR DESCRIPTION	DEPOSIT ELEMENTS
loose sediment	
Pale Greenish Grey 5GY 6/1	$As^{1.5}$ Ag^{1} $Ld^{1.5}$
Light Grey N7 — Light Olive Grey 5Y 5/2	
Light Olive Grey 5Y 5/2 — Pale Olive Grey 10Y 6/2	
Dark Olive Grey 5Y 3/2	As^{1} $Ag^{0.8}$ Ld^{2-} $Dg^{0.2}$
Pale Olive Grey 5Y 4/1	As^{1-} Ag^{2} Ld^{1+}
dark inclusions	$As^{1.5-}$ Ag^{1-} $Ld^{1.5}$ Lso^{0+} Dg^{0+}
	As^{1+} $Ag^{0.75+}$ $Ld^{2.0-}$ $Lso^{0.25-}$
very light grey laminations	
Pale Olive Grey 5Y 4/1	
	As^{1} Ag^{1} Ld^{2-} Lso^{0+}
Greyish Olive Green	$As^{0.5}$ $Ag^{0.5}$ $Ld^{2.5}$ $Lso^{0.5}$
Pale Olive Grey 5Y 5/1	$As^{1.5}$ Ag^{1-} $Ld^{1.5}$ Lso^{0+}
Olive Grey 5Y 5/1	
Dark Greenish Grey 5GY 4/1	$Gmin^{1}$ Ag^{1} As^{1-} Ld^{1+}
Greenish Grey 5GY 3/2	Dg^{0+} Ag^{2} As^{1--} Ld^{1} Lso^{0+}
Dark Olive Grey 5Y 4/1	
Medium Dark Grey N4	
Olive Grey 5Y 4/1	$As^{1.5-}$ $Ag^{1.0-}$ $Ld^{1.5}$ Lso^{0++}
Medium Dark Grey N4	$As^{1.5}$ $Ag^{1.0}$ $Ld^{1.5}$
Light Olive Grey 5Y 6/1	As^{1+} Ag^{2+} Ld^{1-} Lso^{0+}
(brown shades)	$As^{1.5}$ $Ag^{0.5}$ Ld^{2-} Lso^{0+}
Dark Greyish-Olive Green 5GY 3/2	$As^{1.5}$ $Ag^{1.25}$ $Ld^{1.0}$ $Lso^{0.25}$
Medium Grey N5	$As^{2.5}$ $Ag^{1.5}$

of the sediments. Further up the core the composition of the sediments remained more or less stable, and contained a mixture of clay and silt and Limus. Grana minora particles were found only from 204 to 196 cm. In the sediment zone between 29 and 23 cm, a small amount of Detritus granosus occurred.

3.5.2. Water Content and Loss-on-Ignition

The water content and loss-on-ignition, as a measure for organic content, were determined for 51 samples, each consisting of 1 ml of sediment (see section 2.1.). The results are given in Fig. 3.3.

The water content in the samples varied between 21% and 77% of the total wet weight of the samples analysed, and was generally lower below 190 cm. The water content was at a minimum in the bottom sediments of the core. It then increased until the 300 cm horizon, above which it decreased again and remained more or less on the same low level in the samples up the 190 cm horizon. The lower water content values in the older sediments indicated the more compact sediments with poor water-holding properties of the more tightly packed clay sediments predominating especially in the bottom layer of the core. Above 190 cm, the water content increased and remained at a generally higher level than in the older sediments up to the 65 cm horizon. Above this sediment level, the water content declined sharply to a mimimum value in the 40 cm sample, and then increased to a maximum water content in the layer between 29-23 cm. In the youngest sediments, the water content decreased and then rose slightly up to the surface sediments.

Results of the loss-on-ignition analysis revealed a relatively low content of organic matter in the core with values ranging from 2.5% to 17.7% organic matter of the total dry weight in the samples analysed. The organic content throughout most sediments of the core remained relatively stable. The values between 290 and 196 cm were slightly lower than between 196 and 30 cm, and decreased to a minimum of 2.5% at the base of the core. Two pronounced maxima of organic matter content occurred, one between 313 and 295 cm (15.7%) and one near the top of the core between 29 and 23 cm (15.2%). The 29-23 cm layer

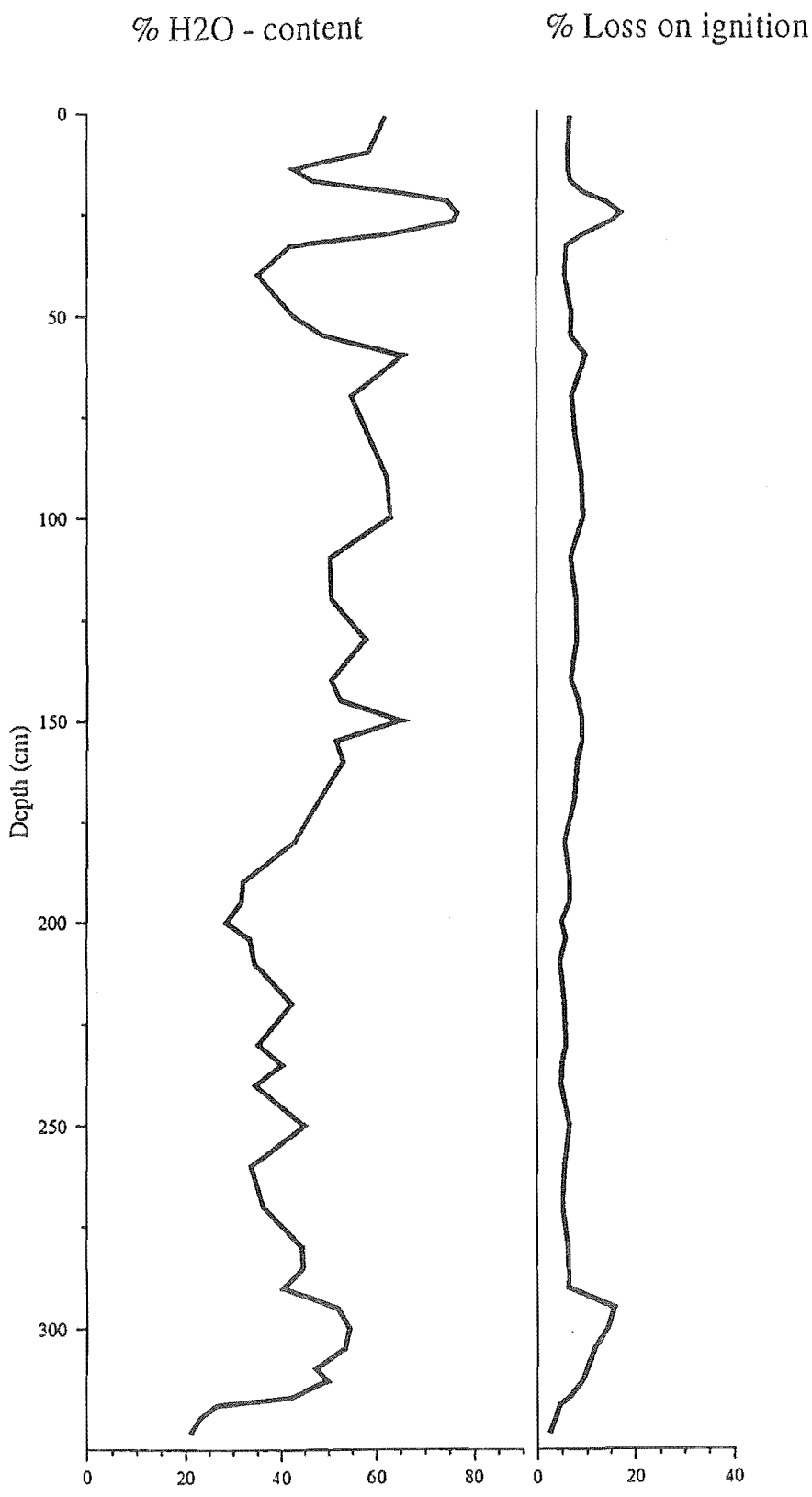


Fig. 3.3. Lake Grasmere: Profiles of water content (as % of wet weight) and loss-on-ignition (as % of dry weight) in the core.

contained the highest amount of organic matter in the core, as well as the highest water content, indicating that this layer was the least compact sediment in the core and contained the lowest amount of minerogenic matter. Throughout the core the profiles of loss-on-ignition and water content were correlated, but fluctuations were generally less marked in the profile of organic matter. The increases in the content of organic matter in the sediments could be due to two processes; a rise in the level of primary production in the lake and/or increased inputs of allochthonus matter provided that the input of minerogenic matter to the sediments remained constant. A fossil pigment analysis was carried out to gain information about the sources of organic matter in the core. The results are presented in Chapter VII.

3.5.3. Unusual Features of the Core Stratigraphy

As mentioned above, the bottom layer of the core contained the lowest amount of organic matter and the deposit element analysis showed that these sediments here consisted mainly of a mixture of clay and silt. This clay/silt layer at the base of the core may have been deposited during a period of naturally accelerated erosion (Bennet, 1939). Accelerated erosion is defined as an increased rate of loss of soil or detritus from the land after plant cover is removed or impaired. The erosion and sedimentation occurring in the mountainous regions of the South Island are very high and sediment yields from some basins in the Southern Alps are amongst the highest in the world (Griffiths, 1981; Whitehouse, 1984). A possible cause for such increased rates of sediment transport is the increased flood flows produced by a greater frequency and/or magnitude of large rainstorms (Beschta, 1985; Grant, 1985, 1989) possibly in connection with damage to vegetation by fire.

The fine sediment at the base of the Lake Grasmere core might have been transported into the lake via Ribbonwood Creek or the Cass River. The Cass River could have flowed into Lake Grasmere 6000 years ago as the form of its fan shows. The clay/silt layer at the base of the core may have originated following a series of frequent large rainstorms in the Craigieburn Ranges (where the headwaters of the Ribbonwood Creek and the Cass River are located), causing severe hillslope erosion with

the resulting sediments collecting in the river. The sediment masses may then have been transported downstream, the coarser sediments depositing in the fans and the margin of the lake, and the remaining fine sediments settling in the deeper parts of the lake. This increased sediment influx had a pronounced influence on the chironomid fauna as will be shown later.

The Grana minora particles in the sediment horizon between 204 and 196 cm could have been deposited by two possible processes. Firstly, the sand deposits might have accumulated as the result of unusual storms, which produced waves or currents of sufficient velocity to move sand out from the shore and deposited it in deeper parts of the lake (Davis et al., 1985a). Secondly, a severe earthquake may have caused landslips in which debris was loosened from the slopes and slipped into the lake. An active, obliquely converging plate boundary between the Australian and Pacific plates, the Alpine Fault, runs the length of the South Island. Many faults traverse the upper Waimakariri basin causing frequent earthquakes in the area (Bradshaw, 1977; Blong & Eyles, 1989).

3.6. Dating of the Sediments

Three samples of the core were radiocarbon-dated (Table 3.1.). The oldest date (318 cm level) revealed that the sediment core from Lake Grasmere spans nearly 6000 years and may not cover the entire history of the lake as it is assumed that the lake originated after the last ice-retreat (Gage, 1959).

Table 3.1. Radiocarbon dates for samples taken from the Lake Grasmere core.

Core Depth (cm)	Laboratory Number	Date
310 - 318	NZ - 7568	5648 + or - 200 yr B.P.
202 - 210	NZA - 353	3410 + or - 120 yr B.P.
42 - 50	NZA - 349	1228 + or - 69 yr B.P.

The radiocarbon-dating was carried out by the Institute of Nuclear Science, Wellington, New Zealand.

3.7. Pollen Analysis

A pollen analysis of the Lake Grasmere core, carried out by Dr. M. McGlone, Landcare Research New Zealand Ltd., Lincoln, showed that Nothofagus was already well established in the catchment area of the lake by 6000 yr B.P. as most samples in the core were dominated by Nothofagus fusca type pollen. An increase of grass pollen at the 30 cm level of the core indicated the arrival of the Polynesians. This zone in the Lake Grasmere core correlates with Zone 6 in the pollen diagram from Kettlehole bog. The presence of European settlers was shown by Pinus and Rumex pollen in the sediments of the core from 6 cm upwards. This record indicates that the last 6 cm of the core were deposited after 1857 when the area was first explored and settled by Europeans (McLeod & Burrows, 1977).

3.8. Diatom Analysis

The fossil diatom flora in samples from the Lake Grasmere core was studied by Dr Margaret Harper, Victoria University, Wellington. The following account is based on her study with additional comments. Fig. 3.4. and Fig. 3.5. were drawn by Dr Harper and reproduced with her permission.

3.8.1. Methods

The diatoms were analysed from 24 samples each consisting of 1 ml of sediment. Samples were taken mostly at 20 cm intervals, except for shorter sampling intervals in the lowermost 20 cm and the uppermost 40 cm of the core. Samples were prepared for analysis as described by Patrick and Reimer (1966). The sediment samples were cleaned with hydrogen peroxide and hydrochloric acid, then washed and the sand fraction removed by decanting, and the volume then made up to 25 ml. 20 µl of the 25 ml suspension were mounted on 12.5 mm diameter coverslips. During analysis, at least 270 frustules were counted at each level along a standard diameter transect (Harper, pers. com.). In Fig. 3.4., diatom numbers are expressed per standard diameter transect of the drop of diatom suspension on the coverslip.

3.8.2. Results and Discussion

The diatom analysis revealed a total of 96 fossil diatom species. Among the most common genera are Fragilaria (undifferentiated F. small. spp., in Girdle View, mostly F. construens varietas, F. construens, F. construens v. subsalina as the dominant species), Cyclotella (with C. stelligera as the most abundant species), Cymbella, Synedra, Achnanthes, Melosira, Nitzschia, Navicula, and Epithemia. Two species colonized the lake only within approximately the last 150 years. Asterionella formosa, and Diatoma elongatum occurred only in the uppermost 10 cm of the core. Harper (in press) suggested that A. formosa and possibly D. elongatum were introduced by Europeans last century. Fragilaria crotonensis first appeared in the sample at the 25 cm horizon (Fig. 3.5.).

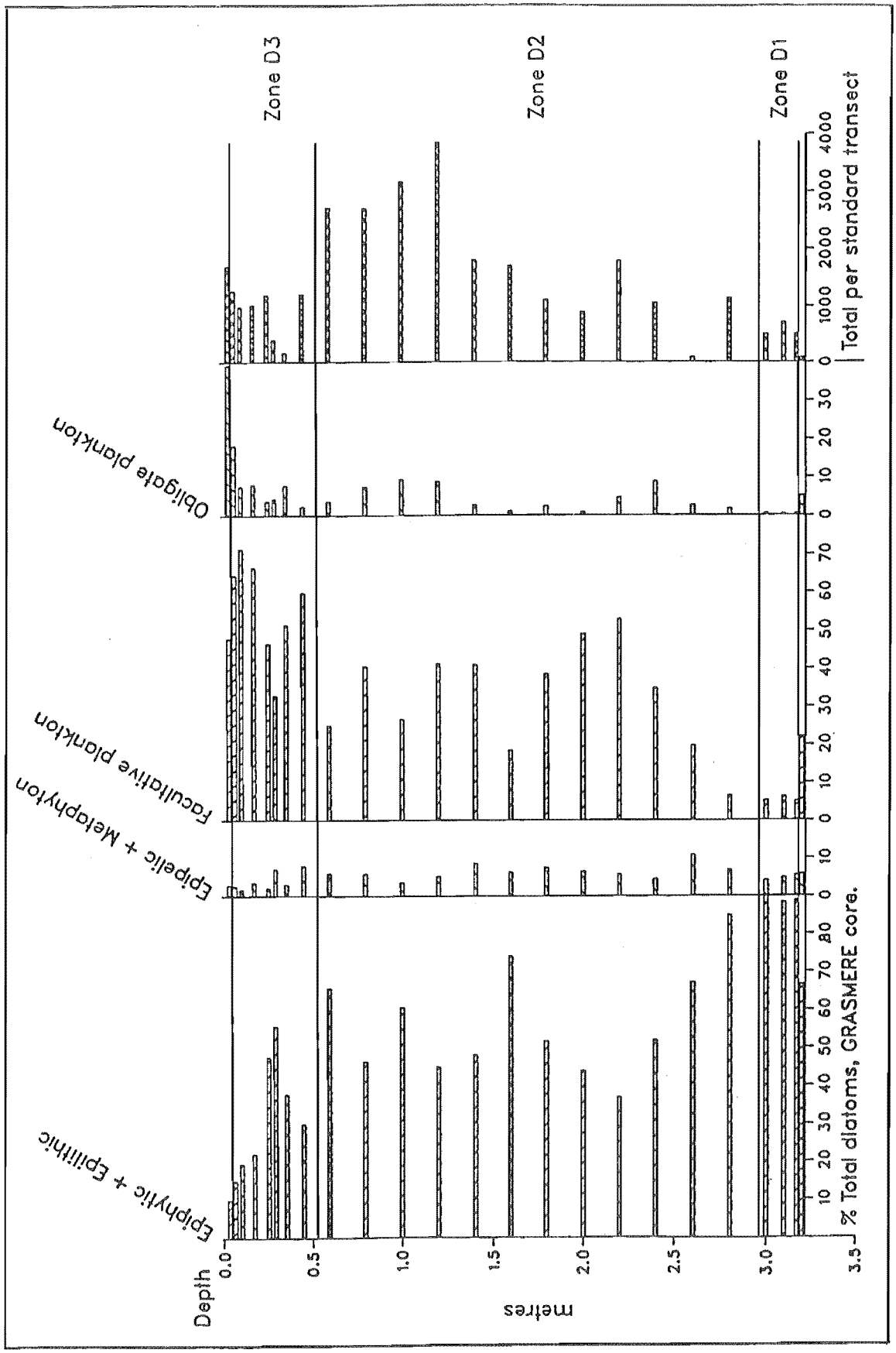


Fig. 3.4. Diatom Profiles from the Lake Grasmere core: Percentages of benthic and planktonic diatoms.

Diatom species often exhibit preferences for a certain pH range (see Foged, 1979; Hustedt, 1937-1939) and fossil diatoms can be used to indicate past trends in the pH of lake waters (Renberg & Hellberg, 1982). Species which are alkaliphil (preferring alkaline waters) predominated at most levels in the Lake Grasmere core (e.g. Fragilaria construens, Synedra ulna, and Nitzschia), but species preferring neutral waters were also abundant in the core samples. Although Sherman (1985) stated that C. stelligera has a pH optimum between 7.5 and 8.0 in Mirror Lake, according to Foged (1979) and Dixit et al. (1991) C. stelligera is indifferent to lake water pH, occurring in a range of pH values but being common in circum-neutral water. Only very few frustules occurred in the Lake Grasmere core of species which prefer acidic water (Harper, pers. com.). The predominance of alkaliphil and circumneutral diatom species indicated that Lake Grasmere has never tended towards dystrophy and has remained slightly alkaline to neutral during the time covered by the sediment record. Alkalibiontic species (mainly Epithemia sorex), which require slightly alkaline waters (Foged, 1979), increased in abundance at the 310 cm horizon and had a more pronounced peak at the 25-27 cm level. These peaks in numbers of alkalibiontic species corresponded with the two maxima of organic matter content in the core. The greatest amount of organic matter (17.7% of dry weight) was recorded in the 25 cm sample (see Fig. 3.2.). These two relatively high levels of organic matter in the core might indicate higher lake productivity during these times. It has been shown that photosynthesis can lead to an increase in the pH of lake waters through withdrawal of carbon dioxide (Tilzer, 1980). Higher numbers of alkalibiontic species at the 310 cm horizon and between 29 and 25 cm might indicate a rise of pH through increased photosynthesis and higher lake productivity.

Besides the pH, the composition of the diatom flora in any given lake is dependent on water chemistry, particularly the amount of dissolved substances, salinity, alkalinity, and specific essential nutrients such as silica, phosphorus, and nitrogen (see Cholnoky, 1968). The interaction of light, nutrients, water depth, turbulence and other physical characteristics determines the kind of habitats available for development of the diatom flora. Shallow lakes in which the light reaches the bottom will support benthic diatom communities, whereas deeper, or more turbulent lakes with seasonally adequate nutrient

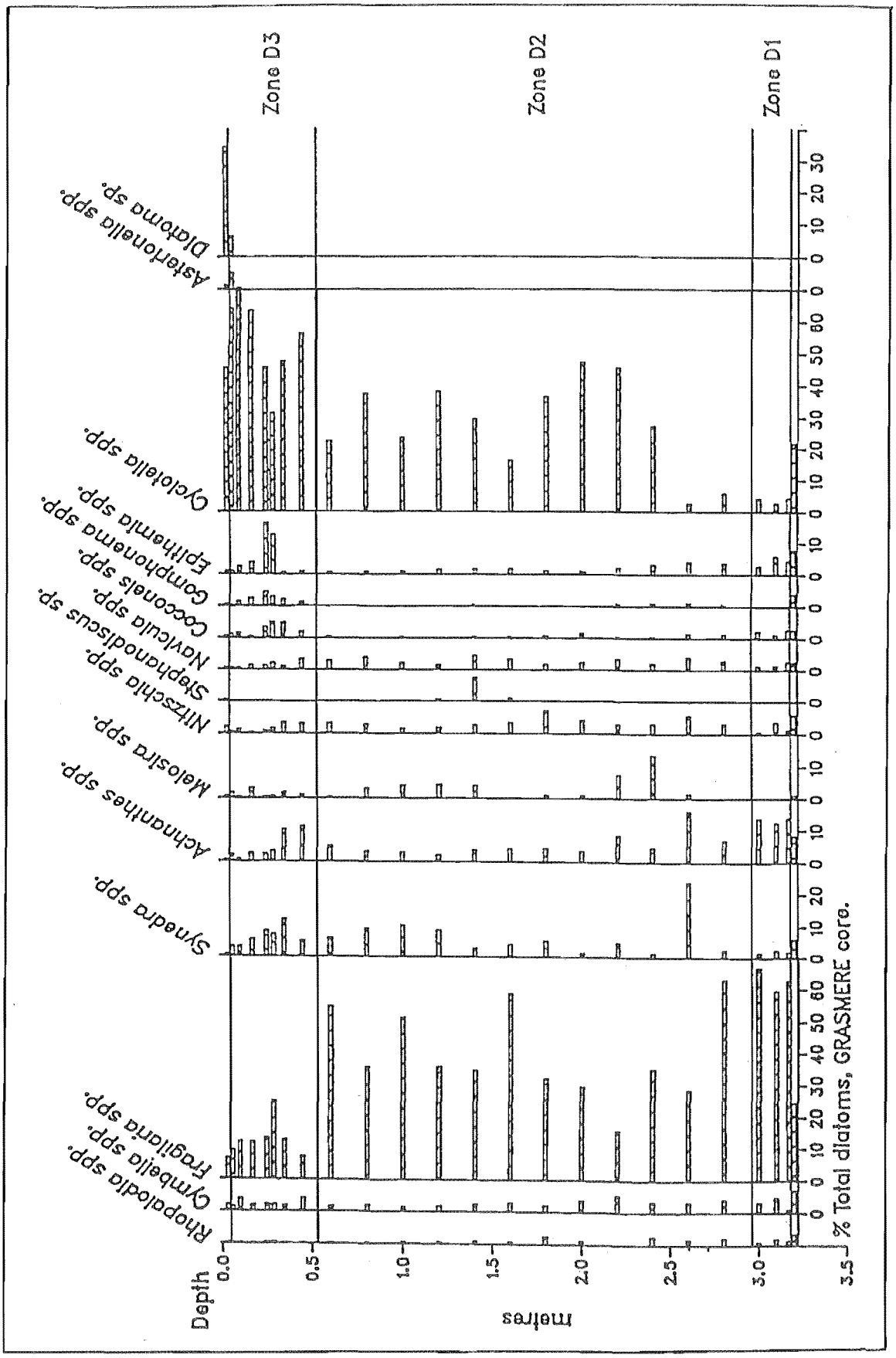


Fig. 3.5. Diatom profiles from the Lake Grasmere core: Percentages of the dominant diatom genera.

supplies will show mainly a greater growth of planktic diatoms (Bradbury, 1986). Therefore, changes in the planktic/benthic ratio of fossil diatom successions can be used to reconstruct changes of the past lake water levels. The planktic/benthic ratio of the fossil diatom succession not only reflects changes in lake morphology but can also be influenced by changes in productivity of the lake or turbidity of the lake waters (Battarbee, 1978). The possibility of changing water levels in the past history of Lake Grasmere was considered to be particularly important in this study, especially in connection with the research on fossil Cladocera.

The distribution of benthic and planktic diatoms in the core from Lake Grasmere is illustrated in Fig. 3.4. Benthic diatoms are divided into attached and mobile benthic forms. Attached benthic diatoms include epiphytic diatoms which are associated with macrophytes (e.g. Fragilaria spp.), and epilithic diatoms which grow on rocks. Mobile benthic diatoms comprise epipelic species which are forms living on the mud surface (e.g. Pinnularia spp.) (Round, 1981), and metaphytic forms which live on plants and the algal organic matter between them.

Percentages (of the total number of diatoms) of epiphytic diatoms throughout the core were relatively high with maxima of abundance between 317 and 280 cm, and at the 160 cm and 60 cm horizons. Lowest abundances of epiphytic diatoms were recorded at 220 cm, 40 cm, and in the most recent sediments (Fig. 3.4.). The relative abundance of epipelic diatoms was stable throughout most of the core but showed a decline in the younger sediments (Fig. 3.4.). Facultative plankton species showed a minimum in occurrence between 280 and 317 cm. Their relative abundance then increased in the sediment layers between 260 and 60 cm, but fluctuated with a minimum at the 160 cm horizon. In the younger sediments, from 45 cm to the top of the core, the relative abundance of facultative plankton species was generally higher, with a slightly reduced occurrence in the 29 and 25 cm horizon in the core. Obligate plankton species occurred throughout the core but with a relatively low relative abundance. A marked increase in the relative abundance of obligate plankton diatoms could be seen in the two top samples of the core (Fig. 3.4.).

The species which were mainly responsible for these trends were Fragilaria spp. for the epiphytic diatoms, and Cyclotella stelligera for the facultative plankton species. The marked increase of obligate plankton species in the youngest sediments was caused by a slight increase in Asterionella formosa and a marked increase in Diatoma elongatum (Fig. 3.5.). Other plankton forms occuring in low numbers belonged to Melosira and Stephanodiscus species.

The small Fragilaria species (F. brevistriata, F. leptostauron, F. pinnata, F. construens), are colonial benthic or epiphytic species (Brugham, 1980) and, because they require light for photosynthesis, are restricted to the photic zone. Therefore, they represent shallow water levels in the lake. In Tasmania, benthic Fragilaria species are generally found in depths less than 1 m in small lakes and ponds, although their depth distribution ultimately depends on water clarity and influx of nutrients (Bradbury, 1986a). Harper et al. (1986) related high abundances of Fragilaria in sediments of Lake Poukawa, North Island, New Zealand, to a probable reduction in lake area due to burning of the surrounding swamp fringe and draining of the lake caused by anthropogenic activities. Fragilaria communities similar to the dominant Fragilaria assemblage in the older sediments of the Lake Grasmere core have been recorded by several authors from late-glacial sediments in the northern hemisphere (Haworth, 1975; Smol & Boucherle, 1985; Rawlence & Senior, 1988). In Barton Board, a shallow (mean depth: 1 m) lake in England, submerged macrophytes declined and phytoplankton numbers increased due to eutrophication of the lake through anthropogenic influences. A diatom analysis of recently deposited sediments showed that an originally epiphyte-dominated diatom community consisting mainly of three species of Fragilaria (F. construens, F. brevistriata, and F. pinnata) was replaced by a planktic diatom community, mainly Melosira. In Barton Broad, this decline in abundance of Fragilaria has been related to the decrease in macrophytes (Osborne & Moss, 1977).

A qualitative examination of recently deposited diatom frustules in surficial sediment samples (collected by the author, see Fig. 8.1. and Fig. 8.2.) from South Island lakes was carried out by Dr. Harper. Her results indicated that small Fragilaria species were found in low numbers in most of the lakes studied, but these species appeared to be

dominant only in the shallow Lakes Emma and Evelyn with a maximum depth of 3 m. In these lakes the diatom flora in the surficial sediment samples was dominated by F. construens var venter and F. pseudoconstruens (Harper, pers. com.). These results demonstrate the predominance of the small Fragilaria species in shallow waters.

Cyclotella stelligera is a cosmopolitan planktonic diatom that tends to characterize oligotrophic to slightly mesotrophic waters. From the occurrence of this species in Tasmanian lakes (Croome & Tyler, 1973), it appears that C. stelligera requires comparatively extensive, limnetic or open-water conditions, clear water, relatively low nutrient levels, and a neutral to slightly alkaline pH (Bradbury, 1986a). These findings are corroborated by a study of diatom assemblages of surface sediment samples from lakes in Western Washington and British Columbia (Brugham & Vallarino, 1989). Using detrended correspondence analysis, their lakes were clustered according to the diatom assemblages of the samples. Lakes whose surface sediment samples were dominated by C. stelligera are deep (average depth: 49 m), clear water lakes with low phosphorus concentrations.

Flint (1970) reported C. stelligera as a characteristic diatom of oligotrophic, large, and deep lakes in the South Island (e.g. Te Anau, Manapouri, Monowai). The results of the study of the diatom flora in surficial sediment samples from South Island lakes revealed that Cyclotella is widely distributed and dominant in several lakes (Harper, pers. com.). These lakes have maximum water depths ranging from 9 m (L. Ida), 17 and 18 m (Lakes Pearson and Letitia, respectively), 28 m (Lakes Katrine and Lyndon), 38 m (L. Mason) to 120 m (L. Tekapo). It appears that Cyclotella occurs as the dominant diatom species in a wide range of water depths in South Island lakes.

The earliest diatom remains (317-240 cm) in Lake Grasmere indicate a shallow, slightly alkaline, oligotrophic lake supporting a moderate littoral diatom flora but few planktic forms. As the flora contained a relatively high proportion of epiphytic and epipelic diatoms at most levels below 50 cm, it appears that Lake Grasmere may have been shallower than at present throughout most of the last 6000 years. Fragilaria was the dominant component of the diatom flora in the older

sediments between 320 and 280 cm and remained relatively important up to 50 cm in the core. As Fragilaria species are mainly epiphytic, macrophytes might have constituted a major part of the ecosystem from about 6000 to ca. 1500 yr B.P.

At the 240 cm horizon, the abundance of Cyclotella stelligera increased and this species constituted an important component of the diatom flora throughout the remainder of the core. The increase in, and subsequent slight fluctuations of, the proportion of planktic forms and total numbers of diatoms between 240 and 50 cm in the core, might indicate a general rise in the water level of the lake, which fluctuated several times (e.g. at 160 cm and 60 cm level). The relative abundance of Fragilaria was generally lowered in samples with a high proportion of Cyclotella. It is also possible that the increase in the importance of the planktic community might have been influenced by a change in chemical conditions of the lake water, e.g. a higher input of nutrients. The abundance of Cyclotella remained low in the older sediments (313-295 cm) when a relatively high content of organic matter in the sediments indicated a higher lake productivity. Therefore, a rise in water depth at the 240 cm level appears to be a more probable explanation for the increase in abundance of Cyclotella this level.

In the youngest sediments, obligate plankton species, especially Diatoma elongatum, showed a marked increase, indicating that the water level might have risen recently to its present depth. This suggestion has to be treated with caution as it is possible that Diatoma elongatum has been introduced by the European settlers (Harper, pers. com.). Flint (1975) recorded Diatoma elongatum as the dominant diatom in the mesotrophic Lakes Selfe (depth: 30 m) and Grasmere (depth: 16 m), and the oligotrophic Lakes Pukaki (depth: 70 m) and Benmore (depth: 120 m). This range of lakes indicates that Diatoma prefers waters of a certain depth (e.g. 10 m and more). Therefore, if Diatoma was introduced by the Europeans, the rise of the water level to the final depth must have occurred earlier, possibly at the 50 cm level. Above this horizon, Cyclotella occurred with relatively stable and high abundances (Fig. 3.5.).

There are several possible causes of an increase in the water depth of Lake Grasmere, such as a partial blockage of the outlet by alluvial gravel or vegetation, perhaps in combination with changes in precipitation, as well as encroachment and damming of the lake by the New Ribbonwood Fan in more recent times. Gage (1959) suggested that the lake in the past extended further eastwards, so that the lake at the sampling site of the core may have been shallower, assuming that the lake volume remained the same and the lake covered a larger area.

At the 140 cm level in the core, an indication of a slight nutrient enrichment of the lake waters can be shown. A sudden increase of the Stephanodiscus hantzschii, from trace levels in the 160 cm sample to 10% of the diatom sum, occurred at the 140 cm horizon. This species was found again only in very low numbers further up in the core. Stephanodiscus hantzschii is a characteristic diatom of enriched lake waters (Lowe, 1974). The single peak in abundance of this species might point to a short-term increase of the nutrient input into the lake during the period this sample was deposited.

A distinct change in the composition of the fossil diatom flora of Lake Grasmere occurred above the 50 cm level in the core. This section of the core (from 50 cm to the top of the core) exhibited frequent changes of the diatom assemblages pointing to an instability of the environment. A period of instability was also indicated by rapid changes in the sedimentation regime (Fig. 3.2. and 3.3.). Above the 50 cm level numbers of diatoms were generally lower (Fig. 3.4.), the percentages of Fragilaria declined (Fig. 3.5.), and there were higher percentages of planktic forms. The combination of these trends might point to an increase in turbidity of the lake waters with a peak in the 35 cm sample. Macrophytes might have become less abundant. Increased turbidity might have been connected to an increased activity of the New Ribbonwood Fan (see Fig. 2.1.). Loss-on-ignition and the water content in the sediment layers between 55 and 33 cm were lower than in the sediments below and above that level which points highly compacted sediments due to an increased mineral input. The minimum of loss-on-ignition (5.7% of dry weight) and water content (35.2% of wet weight) occurred at the 40 cm level (Fig. 3.3.). In the 29 and 25 cm horizons in the core, epiphytic species (mainly Fragilaria) and the alkalibiontic, epiphytic Epithemia sorex increased, corresponding with

a decline of planktic species (Fig. 3.5.). These trends might indicate a decline in turbidity, and/or a short-term lowering of the lake level, together with higher productivity in the lake during the period in which these sediment layers were deposited. The maximum of organic matter in the core at this horizon also indicated an increase in lake productivity and the slightly higher abundance of Fragilaria might point to an expansion of macrophytes during these times. It is possible that this increase in lake productivity has been caused by anthropogenic influence on the lake's catchment. An increase of grass pollen above the 30 cm horizon in the core was reported by McGlone (pers. com., see Chapter 3.7., and Fig. 10.1.), indicating possible burning by Maoris. In the recent sediments (17 to 1 cm), phytoplankton became more dominant, and epiphytic species decreased. This may have been caused by a combination of factors, such as an increase in water depth and turbidity, possibly caused by increased soil erosion through activities by European settlers. The European period is represented in the core by the uppermost 6 cm as indicated by the increase in pine pollen (see Section 3.7.).

The fossil diatom assemblages from two samples (320 cm and 260 cm) exhibited some unusual features. The 320 cm sample originated from the basal clay/silt layer of the core. An extremely low number of diatoms and a comparatively higher percentage of planktic forms point to high turbidity during this period. The 260 cm sample was taken from a medium gray, 2 cm wide sediment layer (Fig. 3.2.), which is stratigraphically distinguishable from adjacent sediment layers. Numbers of diatoms were as low as in the 320 cm sample. In this sample, the proportion of Fragilaria was lower than in the adjacent sediment layers. The relative abundance of Synedra and of Achnanthes was the highest in the core. Achnanthes species are epiphytic and epilithic, and Synedra appears to be mainly planktic (Flint, 1975). The content of water and organic matter (Fig. 3.3.) in the 260 cm sample were very low indicating a comparatively high proportion of minerogenic matter. This caused the low total diatom density and the decline in frustules of the epiphytic Fragilaria species. Synedra as a planktic form might not have been as strongly affected, whereas Achnanthes species might have colonized mainly stones or rocks in the shallow littoral area, therefore receiving sufficient light for growth despite the high turbidity of the lake waters during these times.

To conclude, the composition of the fossil diatom flora from Lake Grasmere changed considerably during the last 6000 years. The dominant epiphytic community was partly replaced by planktic species (between 240 and 50 cm) which became dominant in the youngest sediments (50 cm to 1 cm). This shift in species composition may have been caused by an initial increase in water depth at the 240 cm level and a final rise to the present water depth in the younger sediments as was shown by the decline in Fragilaria, high percentages of C. stelligera, and the marked increase in obligate planktic species in the uppermost sediment layers.

CHAPTER IV

CHIRONOMIDAE IN NEW ZEALAND

Chironomidae are one of the dominant aquatic insect groups of New Zealand with species belonging to six subfamilies: Tanypodinae, Chironominae, Orthocladiinae, Podonominae, Diamesinae, and Telmatogetoninae. The fauna is composed of three elements: common cosmopolitan genera (genera with northern hemisphere affinities) which are mainly found in Chironominae, Orthocladiinae, and Tanypodinae; genera that are probably primitive with a southern landmasses distribution (Podonominae and Diamesinae), and endemic genera (Winterbourn 1980). Five endemic genera occur in New Zealand: Maoridiamesa, Lobodiamesa (Diamesinae), Zealandochlus (Podonominae), Gressittius (Tanypodinae), and Paucispinigera (Chironominae).

The major systematic works on the Chironomidae of New Zealand are those by Hutton (1902), Freeman (1959), Brundin (1966) (who described species of Podonominae and Diamesinae in his transantarctic study of the biogeography of these groups) and Forsyth (1971). Sublette and Wirth (1980) described species from New Zealand's subantarctic islands, including eight monotypic Orthocladiinae genera. Most of the subantarctic species have not yet been recorded from the mainland except for Cricotopus aucklandensis (Boothroyd, 1989).

Wise (1973) listed 72 chironomid species from New Zealand. Cranston and Martin (1989) reported 92 species (including unplaced and undescribed species) in a catalogue of Chironomidae of Australasia and Oceania. An updated check-list was provided by Boothroyd (1988). This list included 83 fully described species, 11 currently unplaced species and nine recorded but undescribed species.

In New Zealand, benthic invertebrate species diversity of lakes (including the chironomid representatives) has been regarded as depauperate in comparison with the diversity found in northern hemisphere lakes (Ashe et al., 1987). Forsyth (1976) attributed the sparseness of the benthic species to the "youth and ephemeral nature of our lakes". This suggestion for the glacial lakes in the South

Island of New Zealand is doubtful because the last glacial advances in Europe and New Zealand (Weichsel- and Poulter advances) came to an end at nearly the same time, ca. 14,000-13,500 yr B.P. (Burrows, 1978, 1984; Nelson et al., 1985)). Thus, glacial lakes in Europe and New Zealand have been in existence for the same period of time. Other more likely causes of the limited diversity might be the small size of the country and its long geographical isolation (Raven & Axelrod, 1972) as well as the possible shortage of refuges during the Pleistocene, which could have reduced species richness on the one hand and aided selection for wide niches on the other (Timms, 1980a).

In a study of 20 lakes of the South Island, Timms (1982) found a total of 16 profundal chironomid species. The maximum was 8 species in 3 lakes (Rotoiti (Nelson), Marymere, and Gault), whereas all the other lakes, including Lake Grasmere, had a very low diversity with an average of 4.7 species. In most of the lakes studied, the dominant chironomids belonged to only three taxa, Chironomus sp., Macropelopia spp., and Cladopelma curtivalva. Timms' study was based on a single or few visits to each lake and Timms (1985) estimated that results gained from samples taken only in one season might underestimate total species richness by as much as 20%. This was not corroborated for the Chironomidae by Timms'(1984) study of the benthic fauna of Lake Pearson. During this study, the lake was sampled for one year every month and Timms found six chironomid species. This was the same number and species composition as in Timms' earlier study (1982). Forsyth (1978) investigated the benthic fauna of seven lakes in the North Island, finding a total of eight chironomid species with an average of five chironomid species per lake. In contrast, the number of profundal chironomid species in three Canadian subarctic lakes of similar area and depth to Lake Grasmere, was considerably higher: in Long Lake, 12 benthic chironomid species were found, 21 in Madeline Lake, and 16 in Grace Lake (Moore, 1980) (This study consisted of a twice monthly sampling of the lake for two years). Therefore, it appears that even if sampling over all seasons is carried out, as was done in Timms'study of Lake Pearson (1984), the profundal chironomid diversity in New Zealand lakes remains lower than that in comparable lakes in the northern hemispere.

A higher number of species in New Zealand lakes is revealed if the whole lake is considered or if the chironomid fauna is studied over long time periods as represented in core material. A detailed study of the macrophyte-associated fauna of Lake Grasmere by Stark (1981) revealed 17 chironomid species, including three unidentified Orthocladiinae species, while Boubee (1983) recorded 13 chironomid species, including littoral and profundal forms, from Lake Maratoto in the North Island. The diversity of chironomid taxa in New Zealand lakes therefore appears to be somewhat higher when the relatively larger number of species in the macrophyte zone, which represents a greater heterogenity of habitats, is taken into account. With regard to chironomid species richness, results comparable with those from the two discussed New Zealand lakes were recorded by Añon Suarez (1991) from a South American lake. In lago Escondido (Argentina), 15 species, including littoral and profundal chironomids, were found. The highest number of species (15), as well as higher larval densities, occurred in the macrophyte zone, whereas only five chironomid species occurred in the zone without vegetation (7-8 m). Compared with the chironomid diversity of lakes in the northern hemispere, the species diversity of Lakes Grasmere and Maratoto, and lago Escondido is still low. For example, Mirror Lake in New Hampshire, USA, has a chironomid fauna composed of 42 littoral and profundal species (Walter, 1985); and gravel pit lake, a human-made small lake in England, had a chironomid fauna composed of 25 species (Learner et al., 1989).

In a preliminary study of the fossil chironomids from a short core from Lake Grasmere, 24 chironomid taxa were found by Schakau (1986). The fossil chironomid fauna in short cores from Lake Monowai was composed of 28 taxa and the remains of chironomids in a Lake Taylor core could be differentiated into 40 taxa (Schakau, 1986). The higher species number found in sediment cores is partly due to the long time periods studied which represent possibly differing ecological conditions over time, and partly due to a possible influx of remains of chironomid taxa from the littoral zone.

The New Zealand chironomid fauna seems to be characterized by a relatively large proportion of monotypic genera, especially in the subfamily Orthocladiinae. Besides the eight monotypic orthoclad genera of New Zealand's subantarctic islands (Sublette & Wirth, 1980),

Boothroyd (1988) described three monotypic Orthocladiinae genera from streams in the Waikato region and his recent collections suggested that there may be more closely related, but distinguishable monotypic genera in New Zealand. The development of monotypic genera reflects different rates of speciation (Cranston & Oliver, 1987). This may be attributed to several factors one of which is geographic isolation. In addition, species with small larvae (such as the monotypic orthoclads described by Boothroyd (1988)) may be able to occupy more restricted habitats. Chironomid species with restricted niches (e.g. substrate or narrow temperature range dependency) may show rapid speciation if they occurred in small localised populations (Mayr, 1970). In groups with broad habitat requirements and widespread populations, there may be a low diversity and rate of speciation, e.g. Chironomus, and Macropelopia (Mayr, 1970).

An example of chironomid species occurring in a restricted habitat can be seen in Lake Grasmere. During qualitative sampling in the lake, it was established that two Orthocladiinae species occurred only in the south-eastern littoral area of the lake. In this area, pebbles and rocks covered with filamentous algae constitute the predominant substrate, and the larvae feed on the algal cover. The two taxa that were found exclusively in this habitat were an as-yet-undescribed Cricotopus species (sp. 25), and Orthocladiinae sp. C (Schakau, pers. obs.; Stark, 1981) which resembles Orthocladiinae sp. c. sp. nov. from Kaniwhaniwha stream (Boothroyd, 1988, unpublished).

4.1. Description of Chironomidae Taxa

In this section, a brief description is given of the chironomid taxa encountered in the different aspects of this thesis and in recent collections to clarify the nomenclature used. Taxa from Blue Lake Australia are not included. Usually it has been only possible to identify chironomid taxa to generic level, except in cases where only one species of a particular genus has been recorded in New Zealand or genera are monotypic. Several as yet undescribed taxa were found, most frequently in the subfamily Orthocladiinae. All forms that appeared to have morphological unity were recorded as separate taxa. This is not only important for taxonomic reasons, but these separate taxa may

display changes within a core which may be of stratigraphic interest when studying sedimentary sequences.

Methods

The procedure to prepare chironomid head capsules for identification and the identification keys used have been described in Chapter II. Photomicrographs were taken to illustrate the distinctive features of most taxa. The photomicrographs are presented in Appendix I (Fig. IV to IX) and are referred to in the text. The terminology follows that of Sæther (1980). Specific taxonomic descriptions are given in italics. Mounted specimens of the larvae or head capsules described are held in the Zoology Department, University of Canterbury.

TANYPODINAE

Head capsules belonging to this group could be distinguished into seven taxa. These are Apsectrotanypus (Fig. VII-K), Gressittius antarcticus (Fig. VII-N), Macropelopia, Ablabesmyia mala, nr. Pentaneura (Fig. VII-L), Tanypodinae sp.I (Fig. III-U, Fig. VII-M), and Tanypodinae sp. II (Fig. VII-J).

Three of the tanypod taxa recorded belonged to the tribe Macropelopiini. Identification of Macropelopiini species is difficult because the taxonomic status of the group is still unresolved (Cranston & Martin, 1989). The association of Macropelopiini taxa with generic or species names remains therefore tentative in this thesis. Ten species of Macropelopiini have been described as adults in New Zealand (Hudson, 1892; Hutton, 1902; Freeman, 1959; Sublette & Wirth, 1980), but only one species, Gressittius antarcticus, is known in its larval form (Forsyth, 1971). Stark (1981) collected two pupal types of Tanypodinae from Lake Grasmere, the most common pupa belonging to Gressittius antarcticus. The respiratory trumpet of this species, with its wide and convoluted trachea, is very distinctive (see Sublette & Wirth, 1980, p. 335). Several of these respiratory trumpets were found in samples from the core establishing that this species occurred in Lake Grasmere in the past. Fossil head capsules of this species were separated from the other two Macropelopiini taxa on the basis of the

differing number of teeth on the dorsomentum. Fossil head capsules possessing dorsomental plates with 6 teeth were placed in Gressittius antarcticus (see Stark, 1981, p. 174, Fig. 6.11. C.). The second Tanypodinae pupal type collected by Stark (1981) was placed by him in Macropelopia umbrosa. Larvae, which were tentatively associated with this pupa by Stark (1981) had dorsomental plates with only 4-5 teeth. Martin (in Timms, 1982) suggested that larvae of this type possess characters of Apsectrotanypus. Fittkau and Roback (1983) regard the small number and the large size of the dorsomental teeth of this type as sufficient to distinguish it from most other Tanypodinae genera. In this thesis, head capsules whose dorsomenti had only 4-5 teeth were referred to as Apsectrotanypus, whereas head capsules with 7-8 teeth were placed in Macropelopia. One important morphological character of Apsectrotanypus is its short second antennal segment. Martin (1987) lists the antennal segment 2 as about 2.5x as long as wide, and that of Macropelopia as about 3.5x as long as wide. Measurements of living larvae of Macropelopia from Lake Grasmere agreed with Martin's key, but recent larvae of Apsectrotanypus exhibited a length of their second antennal segment of being 3x as long as wide without an especially deeply set style, which is another morphological character of this genus as described by Fittkau and Roback (1983). Further taxonomic studies of this group are certainly required, which may result in the classification of a new genus for the specimens referred to in this thesis as Apsectrotanypus.

The genus Ablabesmyia is represented in New Zealand so far by only one species, A. mala (Cranston & Martin, 1989). Larvae of Ablabesmyia are identifiable by the multisegmented base of the maxillary palp. Fossil head capsules were matched with living larvae found in Lake Pearson, which is situated closely to Lake Grasmere. Although Stark (1981) recorded larvae of this species from Lake Grasmere, no living larvae were found by the author in qualitative collections from this lake.

Living larvae of the taxon nr. Pentaneura from Lake Grasmere key to Pentaneura in Wiederholm (1983), but possess neither the long anal tubules nor the large preanal setae, mounted on humps, which are characteristic of the genus Pentaneura. One described species, Pentaneura harrisi, has been recorded from New Zealand (Freeman, 1959; Forsyth, 1971) but this species is now placed as Zavrelimyia harrisi

by Cranston and Martin (1989). Larvae of nr. Pentaneura do not fit entirely into this taxon either because they lack a bifid claw on the posterior parapod and do not possess an exceptionally broad pseudoradula (Fittkau & Roback, 1983). The distinction between nr. Pentaneura and Ablabesmyia was difficult to make in the fossil material. Only head capsules which had retained the multi-segmented base of the maxillary palp were placed in Ablabesmyia, the remaining fossil Pentaneurini head capsules were recorded as nr. Pentaneura.

Head capsules of the type Tanypodinae sp. I were found only as fossils in the sediments of Lake Grasmere. A distinctive morphological feature of this type is the ligula with four darkly pigmented teeth, the outer teeth being much larger and 2x as long as the pair of middle teeth. The ligula is 2x as long as its apical width and narrowed apically of the basal 1/3. The paraligula is slender and nearly as long as the ligula. It is bifid consisting of the apical point and one inner tooth. The dorsomentum has four teeth. The apex of the ventromentum is clearly defined and is "onion"-shaped. The M-appendage, the pseudoradula, and labial vesicles could not be seen in the fossil material. If these morphological characters were lacking in the larvae from which these fossils originated, their absence could indicate the possibility that head capsules of Tanypodinae sp. I might not represent a separate taxon but instead an early instar (presumably the second) of one of the Macropelopiini taxa (Mozley, 1979; Roback, 1989). Second instar larvae of Procladius (Mozley, 1979) and Djalmabatista (Roback, 1989) possess menti without as yet formed M-appendages, pseudoradulas, and labial vesicles, and a well defined apex of the ventromentum. Contrary to this suggestion, the good preservation as fossils of the head capsules of Tanypodinae sp. I may indicate that these head capsules are later instars of a separate species, particularly as fossil head capsules of Tanypodinae generally do not preserve as well as head capsules of other chironomid subfamilies (Walker et al., 1984). Of the antenna, only the basal segment remained in the fossil material of Tanypodinae sp. I, its length being nearly that of the mandible. The mandible has a slender apical tooth, which is 3x as long as its basal width. Three lateral teeth are discernable with the middle tooth being the smallest.

Head capsules of Tanypodinae sp. II occurred as fossils in the sediment samples from the Lake Monowai core (Schakau, 1986) and in the surficial sediment samples from Lake Matheson. The head capsules are narrow with a cephalic index (ratio of maximum width: length) of approximately 0.65. The dorsomentum is without teeth. The ligula has four teeth, all teeth being of equal length and size. The paraligula is half the length of the ligula, and bifid with the outer point 2x as long as the inner point. The mandible is moderately curved, the apical tooth 3x as long as the basal width and 1/4 of the length of the mandible, and there are two lateral teeth of which the accessory tooth is only slightly smaller than the basal tooth. Complete antennae have not been found in the fossil material, but the basal segments of the antennae retained in some of the head capsules studied were approximately 1/3 the length of the head capsules.

PODONOMINAE

Podonominae head capsules in the fossil material could be differentiated into Parochlus and Podonomus. Identification of the fossil head capsules was facilitated by comparing the fossil material with recent larvae from the two genera which had been found in several stream sites in the Cass area (Coll. R. Death).

Parochlus (Fig. V-L, Fig. VII-O) is easily recognized by the structure of the mentum with the median tooth being longer and broader than the first of the seven pairs of lateral teeth. Specific determination of Podonominae larvae is not possible but Stark (1981) collected pupae of P. spinosus Brundin (1966) from the stony shore at the south-eastern end of Lake Grasmere. Thus, it is possible that the fossil head capsules of Parochlus also belong to this species.

Podonomus head capsules possess a mentum with one median tooth and seven pairs of lateral teeth. The median tooth and the first two pairs of lateral teeth are more or less of equal length and size but the third pair of laterals protrude and are longer than all other lateral teeth. It was not possible to identify the fossil material to species level.

DIAMESINAE

In this thesis, all Diamesinae taxa are listed under the tribe Heptagyini. This is in accordance with Stark (1989) and Boothroyd (1988) but not with Cranston and Martin (1989) who placed Maoridiamesa in the tribe Lobodiamesini.

Head capsules belonging to Maoridiamesa (Fig. V-M) were the most common of the Heptagyini. Five species are described from New Zealand, but a specific determination of the fossil material was not possible. Besides Maoridiamesa, four as yet undescribed Heptagyini taxa occurred: nr. Limaya (Fig. V-K), Heptagyini sp. I (Fig. VI-H), Heptagyini sp. II (Fig. VI-I), and Heptagyini sp. III (Fig. IX-C).

Head capsules belonging to nr. Limaya have been found as fossils in very low numbers in samples from the Lake Grasmere and Lake Monowai cores. In addition, larvae had been collected in streams on Banks Peninsula, the Glentui River (Coll. R.L.C. Pilgrim) and streams in the Cass area (Coll. R. Death). Larvae of this type were designated as nr. Limaya (Brundin, 1966) because of the similar menti of the two taxa. Limaya is only recorded from Chile and Patagonia. Several of the morphological features of the New Zealand taxon suggest that this may be an endemic genus. The head capsule of nr. Limaya is pale brown with well developed dark occipital margins with dorsolateral incisions. The characteristic features are : *mentum very pale, with one wide median tooth and 5 pairs of lateral teeth; median tooth partially fused with first pair of lateral teeth, wider than combined width of one side of laterals; second pair of laterals on same plane as median tooth, as high as first pair of laterals, the remaining 3 pairs set on a lower level with the 3rd lateral projecting above the 2nd and 4th lateral. Ventromental plates fused medially and forming the ventral surface of the mentum.* The ligula and paraligula of the premento-hypopharyngeal complex are not shaped as 3 brushes of hair-like processes as in Limaya (Brundin, 1966). The ligula of nr. Limaya is reduced, consisting of 2 small scales (?); the paraligula consists of a group of broad blade-like setae. *Pecten epipharyngis formed of 3 broad lamellae. Premandible simple. Mandible with apical tooth shorter than combined width of 4 inner teeth. Seta interna fan-shaped, apically branching. Antenna 6-segmented, segment 2 hyaline, terminal segment*

hairlike. Hyaline blade shorter than flagellum, style present on the 3rd segment.

Head capsules of Heptagyini sp. I (Fig. VI-H) have been found only in the surficial sediment sample from Lady Lake. This taxon is only tentatively placed in Heptagyini. The characteristic features are: *mentum with double median tooth and 5 pairs of lateral teeth; with paler, less sclerotized longitudinal grooves appearing as striations; ventromental plates present, beard absent. Antenna with only 3 segments of which segment 3 is the longest. First segment 2x as long as basal width is wide with ring organ apical of basal 1/2; segment 2 as long as basal width, and 3rd segment 13x as long as basal width, segment 3 hyaline and annulated.*

Larvae of Heptagyini sp. II were collected from a small creek on Bridge Farm, Dunsandel (December 9, 1990). The substrate of the sampling site consisted of pebbles covered with filamentous algae. The head capsule of this taxon is yellowish brown, with occipital margins only weakly developed. The characteristic features are: *mentum with median tooth and 9 pairs of laterals, ventromental plates weakly developed. Ligula and paraligula consisting of brushes of very fine setae. SI bifid, other setae on labrum simple; pecten epipharyngis consisting of 5 scales, the outer 2 pairs pointed, the median scale rounded apically and longer than the others. Chaetulae laterales forming arched group on either side of pecten epipharyngis. Premandible with two apical teeth and one broad inner tooth. Mandible with short apical tooth, shorter than combined width of 3 inner teeth. Apical part of mola darkened; mola serrated. Seta subdentalis lancet-shaped, deeply set. Seta interna consisting of originally 1 broad seta dividing into 5 branches, apically serrated. Antenna 5-segmented, basal segment nearly 2x as long as segments 2-5 together, segment 3 and 4 of similar length; Lauterborn organs small; blade shorter than flagellum; ring organ in basal 1/3 of basal segment. Parapods well developed; posterior parapod with simple, dark claws; procercus as long as wide with 6 anal setae and 2 subapical setae.*

One larvae of Heptagyini sp. III (Fig. IX-C) was collected from Middle Bush Stream (Coll. R. Death, October 23, 1987). The head capsule of this larva has well developed dark occipital margins with dorsolateral

incisions. The characteristic features are: *mentum with broad median area without teeth, nearly as wide as 1/2 width of flattened mentum; 6 pairs of lateral teeth present. Ventromental plates well developed. Antenna 5-segmented, basal segment shorter than segments 2-5 together. Segment 2 slightly longer than combined length of segments 3-5, segment 3 appears to be annulated. Pecten epipharyngis consisting of 3 pointed scales, difficult to separate from the similarly formed chaetulae lateralis; premandible with one apical broad tooth. Ligula and paraligula appear as three fine brushes of hair-like processes. Mandible with slender apical tooth, 1.8x as long as combined width of 4 inner teeth; seta subdentalis short and pointed; seta interna consisting of 3 long simple setae; outer margin of mandible crenulated. Anterior parapods fused, apically divided into 2 lobes, with each lobe bearing a circle of claws. Posterior parapods separate, each with crown of claws. Procercus shorter than wide, with 6 anal and 1 subapical, setae present.* This taxon is similar to Lobodiamesa in many features (Brundin, 1966) but Lobodiamesa has a 4-segmented antenna, a smooth outer margin of the mandible, and an arched mentum.

Heptagyini II and III were not found in the fossil material or in recent collections from Lake Grasmere. I have included photographs and the short description of the larvae in this thesis because of their interesting morphological features.

ORTHOCLADIINAE

A total of 17 orthoclad taxa was found in the samples from the Lake Grasmere core (11 taxa, see Table 5.1.), and the surficial sediment samples from South Island lakes (13 taxa, see Table 8.5). Additionally to microphotographs of orthoclad taxa from Lake Grasmere, microphotographs of Orthocladiinae head capsules from core samples from Lake Monowai (Schakau, 1986) are presented in Fig. IV in Appendix I. Orthocladiinae presented great problems of identification. The highest number of as-yet-undescribed taxa could be distinguished in this subfamily.

Head capsules belonging to Orthocladiinae sp. IX (Fig. IV-F, Fig. IX-D) were the most common Orthocladiinae head capsules found in the South Island. One female from Lake Grasmere, collected from amongst the macrophytes on November 11, 1984, was reared and could only be placed as near Paralimnophyes using Sæther's (1977) key. This orthoclad taxon corresponds to Stark's Orthocladiinae A (1981) and Boubee's orthoclad I (1983).

Larvae of this type are small to medium sized, up to 5.2mm long. The body and head capsule are coloured yellowish to yellowish brown. This taxon can be separated from other Orthocladiinae by the two median teeth of the labial plate that project considerably above the five pairs of lateral teeth. All teeth are arranged on a straight plane and are strongly sclerotized. *Ventromental plates and a weak beard, consisting of 7-8 fine setae, are present. Antenna 5-segmented; segment 4 slightly longer than segment 3. Lauterborn organs small; blade shorter than flagellum; ring organ in basal third. SI of labrum simple with apical tooth, SII - SIV simple. Pecten epipharyngis consisting of 3 broad scales of which the outer ones are pointed and the median scale rounded. Premandible bifid and of broad structure. Mandible with apical tooth shorter than combined width of 4 inner teeth; seta subdentalis lancet-like; seta interna with 7 branches, all of them serrate throughout their length; mola smooth. Parapods well developed. Procercus as long as wide, with 7 anal setae. Anal tubules shorter than posterior parapods.*

Head capsules of the Cricotopus type could be classified as belonging to three taxa: Cricotopus sp. (possibly embracing two species), Cricotopus SRV sp. 25 , and one Cricotopus taxon which is tentatively placed in C. aucklandensis.

Stark (1981) recorded larvae of Cricotopus zealandicus and of Syncricotopus pluriserialis from Lake Grasmere, with C. zealandicus occurring in greater abundance than S. pluriserialis. The differentiation of the larvae in Stark's study was possible through positive associations with reared adults. Syncricotopus pluriserialis is now placed in Paratrichocladius (Cranston & Martin, 1989). In the fossil material, species identification was impossible; and if these two taxa were present as fossils, a distinction could not be made

between them because of the similar menti. Thus, all head capsules with a narrow median tooth and 6 pairs of lateral teeth, which are characteristic of both these taxa, are referred to in this thesis as Cricotopus sp. (Fig. VI-A, Fig. IX-A).

Head capsules of Cricotopus sp. 25 (this species was compared with Australian Cricotopus species in the collection of V. Pettigrove, Rural Water Commission of Victoria, and differed from all Cricotopus specimens collected in Australia; SRV code-number, V. Pettigrove, pers. com.) can easily be distinguished from Cricotopus sp. by the wide median tooth of the mentum (Fig. VI-B). Living larvae of this taxon have been found amongst filamentous algae on the surface of rocks on the stony shore of the south-eastern shore of Lake Grasmere. The median tooth and first pair of laterals appear to be fused in all specimens studied and project anteriorly above the remaining 5 pairs of lateral teeth. *Median tooth and first laterals as wide as combined width of one side of lateral teeth. Setae submenti long, nearly reaching to apex of median tooth. Mandible with apical tooth shorter than combined width of 3 inner teeth. Seta interna consisting of 6 branches, finely serrated apically. Outer margin of mandible smooth, mola with weak spines. Antenna 5-segmented; premandible with broad apical tooth.*

Head capsules, which have been designated C. aucklandensis, have been found in surficial sediment samples of several lakes in the South Island (Fig. 8.4.). C. aucklandensis was originally described from the subantarctic islands (Sublette & Wirth, 1980) but Boothroyd (1989) recorded this species from several Waikato streams and rivers. The mentum of C. aucklandensis possesses a broad median tooth but this is not as wide as the median tooth in Cricotopus sp. 25; the width of the first lateral teeth are much less than half the width of the median tooth.

The genus Rheocricotopus has not been described from New Zealand. Living larvae of this type collected in Lake Grasmere and associated fossil head capsules have been designated Rheocricotopus because they keyed to Rheocricotopus in Wiederholm (1983) and Cranston (1982). Stark (1981) and Timms (1982, 1983) recorded larvae designated as "Rheocricotopus" from Lake Grasmere and several South Island lakes,

but adults that possessed the generic features of this genus (see Brundin, 1956b) had not been found by Stark (1981) in hand-net or light trap collections from Lake Grasmere.

Morphological characters of Rheocricotopus from Lake Grasmere generally correspond with those described for Rheocricotopus in Cranston (1982). The mentum of larvae from Lake Grasmere displays the 2 median teeth, 5 pairs of lateral teeth, and well developed ventromental plates with a strong beard characteristic of this genus; SI is bifid, and the apical tooth of the mandible is shorter than the combined width of the 3 inner teeth. There are, however, several features of Rheocricotopus larvae from Lake Grasmere which are different: the antenna possesses very distinct Lauterborn organs, extending to the mid-point of segment 4; SII on labrum is composed of well developed setae on tubercles; the premandible has 2 apical teeth; and the seta subdentalis of the mandible is pointed without the apical hook characteristic for this genus.

Rheocricotopus from Lake Grasmere appears to be similar to the larva of Orthocladiinae sp. a (tentatively named Naocladius) described by Boothroyd (1988). The larva of Naocladius has a mentum with a double median tooth, 5 laterals, well developed ventromental plates and beard, a bifid premandible, and a lancet-shaped seta subdentalis, but Rheocricotopus from Lake Grasmere differs from Naocladius by the distinct Lauterborn organs and the shape of the labral seta SII.

Because of the these taxonomic difficulties, head capsules found in surficial sediment samples from South Island lakes, which exhibit menti with 2 median teeth, 5 laterals, and well developed ventromental plates and beard, are referred to as Orthocladiinae sp. VIII (see Chapter VIII).

The genus Eukiefferiella is represented in New Zealand by one described species, E. heveli, from the subantarctic islands (Sublette & Wirth, 1980), and one new species described by Stark (1981, unpublished). In this study, possibly 3 taxa belonging to Eukiefferiella could be distinguished in the fossil material and in larvae from recent collections.

Larvae, collected by hand-net in Lake Grasmere (pers. coll.), as well as from streams in the Cass area (Coll. R. Death) and near Westport (Coll. P. Ryan) as well as fossil head capsules from the Lake Grasmere core and surficial sediment samples from several South Island lakes, could be placed in the Eukiefferiella claripennis group (Fig. II-N). Larvae of this taxon are small, up to 3mm long, with their body coloured yellow and well developed parapods. *Procercus present, slightly higher than wide, bearing 6 anal setae; basal subapical seta conspicuous, arising anterior to the side of the procercus. Head capsules dark yellowish-brown; antenna 4-segmented with basal segment 1.5x as long as combined length of segment 2-4; ring organ in first 1/3 of basal segment; blade shorter than flagellum, style as long as segment 3; Lauterborn organs present. SI - SIV on labrum simple, pecten epipharyngis consisting of 3 scales, premandible broad with 1 apical tooth, brush absent. Mandible with short apical tooth and 3 inner teeth, seta subdentalis lancet-shaped, mola with 2 spines. Mentum very distinct with a double median tooth and 5 pairs of lateral teeth; mentum strongly sclerotized, with irregular longitudinal bands of dark sclerotization alternating with lighter bands.*

Fossil head capsules belonging to Eukiefferiella sp. (Fig. IV-B) have been found in surficial sediment samples from Lakes Grasmere, Taylor, Shepard, Ohau, Brunner, and Lady Lake (see Appendix, Table III.2) and in core samples from Lake Monowai. The mandible of this taxon has spines on the mola; the premandible has one broad apical tooth; the mentum appears to be similar to that of the E. bavarica group (Simpson & Bode, 1980) with 2 pointed, spade-shaped median teeth.

Orthocladiinae sp. 2 (Fig. IV-A) is possibly Eukiefferiella, as fossil head capsules of this type found in core samples from Lake Monowai exhibit the serrated mola of the mandible and a premandible with one broad apical tooth. The mentum looks similar to that of the E. coerulescens group (Wiederholm, 1983) with the median tooth and first pair of laterals projecting above the remaining lateral teeth.

Head capsules of Corynoneura (Fig. III-S) occurred in core samples from Lake Monowai and Lake Taylor (Schakau, 1986) and in surficial sediment samples from Lakes Brunner and Ohau. Living larvae have been collected from ponds in Hamner Springs (21/6/1991). Corynoneura head

capsules are easily recognized by the triangular mentum with 3 median teeth of which the central tooth is much smaller than the 2 outer teeth, and 5 pairs of lateral teeth. Only one species, C. donovani (Forsyth, 1971), has been described from New Zealand.

The following taxa have been found as fossils only. The distinction between the taxa is based mainly on the menti of the head capsules.

Matakiri (Orthoclad. sp. b. gen. nov.) (Fig. VI-C) has been described by Boothroyd (1988, unpublished). The larva of this genus has a distinct mentum with a broad double median tooth and 3 pairs of lateral teeth, with less sclerotized longitudinal grooves appearing as striations and ventromental plates absent. Fossil head capsules which have been placed in this taxon were found in core samples from Lake Grasmere and surficial sediment samples from Lakes Brunner, Alexandrina, and Lady Lake.

Head capsules placed in nr. Synorthocladius (Fig. VI-E) possess 2 tall median teeth and 4 pairs of lateral teeth. The beard characteristic of Synorthocladius is apparently absent in the South Island material. Head capsules were found in the Lake Grasmere and Lake Taylor cores and surficial sediment samples from several South Island lakes (see Appendix, Table III.2).

Orthocladiinae sp. I (Fig. II-O, Fig. VI-D) head capsules appeared in core samples from Lake Grasmere. The mentum of this taxon has one median tooth and 5 pairs of laterals. The median tooth is peaked and about 2x as wide as first laterals. The mentum of Orthocladiinae sp. I appears to be similar to that of Pseudosmittia sp. in Roback and Coffman (1983, p.39).

Orthocladiinae sp. 13 (Fig. IV-E) head capsules were found in Lake Monowai core samples and surficial sediment samples from Lake Ohau. Head capsules of this type possess a mentum with a broad double median tooth, as wide as 1/2 the width of the mentum, and 4 pairs of lateral teeth. The ventromental plates are long and narrow; the mandible has a short apical tooth and 3 inner teeth, and one small extra tooth situated dorsally of the first inner tooth, the seta interna has 7-8 very long branches.

Orthocladiinae sp. XIV (Fig. II-M) occurred in Lake Grasmere core samples and surficial sediment samples from Lakes Coleridge, Haupiri, Brunner, and Lady Lake. The mentum has one narrow median tooth and 5 pairs of laterals.

Orthocladiinae sp. XV (Fig. VI-F) head capsules were found in samples from the Lake Grasmere core and in surficial sediment samples from several South Island lakes (Fig. 8.4.). The mentum of this taxon has a wide median tooth (possibly a worn-down double median tooth) projecting above the 4 pairs of lateral teeth; the premandible has 2 apical teeth and one inner tooth, the mandible exhibits one broad, rounded apical tooth and 2-3 inner teeth. Orthocladiinae sp. XV may be the fossil of Orthocladiinae sp. C (Stark, 1981), but whereas head capsules of Orthocladiinae sp. C are very darkly pigmented, fossil head capsules of Orthocladadiinae sp. XV are very pale in comparison. Thus, Orthocladiinae sp. XV is kept as designation for these particular head capsules.

The placement of the two chironomid taxa described in the next section, is uncertain. Both taxa are placed tentatively in the subfamily Orthocladiinae but possess morphological features which are unusual for this subfamily.

Fossil Orthocladiinae sp. V (Fig. III-T, Fig. IV-D, Fig. IX-E) head capsules have been found in core samples from Lakes Grasmere, Monowai, and Taylor, as well as in surficial sediment samples from Lakes Coleridge and Brunner (see Appendix, Table III.2). Living larvae have been found in streams in the Cass area (Coll. R. Death) and in the gut contents of Nanochorista philpotti, collected from streams on the Banks Peninsula (Coll. R. Pilgrim).

Studying the recent larvae of this taxon revealed that this taxon may be misnamed and perhaps should be designated as Heptagyini sp. V. Several morphological features of Orthocladiinae sp. V are similar to those of nr. Limaya, particularly the shape of the ligula (2 small bifid scales ?) and paraligula (arrangement of group of broad setae), and the structure of the antenna.

The characteristic features are: *larvae small, up to 2.5mm long. Parapods well developed; anterior parapods bearing pectinate claws, posterior parapods simple claws; procercus slightly longer than wide, with 3 anal setae and 1 subapical seta. The head capsule is pale yellow; the mentum with 2 broad median teeth and 3 pairs of lateral teeth, consecutively becoming smaller laterally; median teeth as wide as 1/2 of width of mentum. Mandible strongly curved, with slender apical tooth, shorter than combined width of 3 inner teeth; mola smooth, apex of mola darkened; seta subdentalis apically pointed, seta interna with 7-8 simple branches. Labral setae SI - SIV simple, SII a robust blade; pecten epipharyngis apparently with 3 broad scales; premandible with 2 apical teeth. Antenna 6-segmented, basal segment short, 1.6x as long as wide, segment 2 shorter than segment 3, terminal segment hairlike; blade wide and blunt, reaching apex of segment 4; style with knob-like apex present on apex of segment 1.*

Orthocladiinae sp. C (Fig. IX-B) has been found only on the stony shore at the south eastern end of Lake Grasmere. Stark (1981) tentatively placed these larvae in the subfamily Orthocladiinae, but suggested that this taxon may represent a new subfamily. Boothroyd (1989) found larvae (Orthocl. sp. c. gen. nov.) in Kaniwhaniwha stream, Pirongia, which are similar to Orthocladiinae sp. C. He argued that although the larva and pupa of Orthoclad. sp. c. possess characteristics which are very different from other orthoclad genera, the adult has features relating it to the Orthocladiinae. After studying larvae from my collection, I tend to agree with Stark, especially because there are differences between the Lake Grasmere and the Pirongia larvae.

The characteristic features are: *larvae small to medium sized, up to 4.3 mm long, body coloured darkly purple to brown; parapods well developed, each bearing an apical crown of claws; procercus absent, a group of 6 anal setae arising from the body wall. Two setae arising anterior close to bases of anal setae, one of which is approximately half the length of the anal setae, the other setae very fine and short.*

The head capsule is dark brown, some specimens with well a developed occipital margin as in Maoridiamesa. Mentum with broad median tooth,

wider than first pair of laterals, and 4 pairs of lateral teeth; median tooth and first pair of laterals paler than strongly sclerotized rest of the mentum, striations apparent in median area of mentum caused by longitudinal grooves of weaker sclerotization. Ventromental plates present, beard with 4 strong setae branching apically. Mandible with blunt apical tooth, shorter than combined width of 3 inner teeth, third and fourth inner teeth rounded; seta subdentalis apically pointed, apex of mola forming a hook ventrally positioned before seta subdentalis; mola with spines pointing outwards, seta interna with 4 branches, being consecutively longer, apically weakly serrated. The prementо-hypopharyngeal complex is difficult to discern, but the ligula is formed apparently of 2 scales apically serrated, with the paraligula appearing as a group of relatively long setae; this morphological feature is more similar to Diamesinae than to Orthocladiinae. The labral setae SII - SIV are arranged in a transverse row, all of them are simple. SI positioned anteriorly between SII and SIII, clearly bifid. Nine pairs of pectinate chaetae present on labrum. Pecten epipharyngis formed of 3 broad scales with 2 chaetulae laterales of similar shape present, giving the appearance of 5 scales. Premandible with 2 rounded apical teeth and one inner tooth. The antenna is 4-segmented, the basal segment only slightly longer than its basal width, ring organ at apex of first 1/2 of basal segment, Lauterborn organs small; blade shorter than flagellum, bifid, the longer branch of the blade appears to be annulated.

Several morphological features of this larvae are similar to the Heptagyini: the prementо-hypopharyngeal complex, the arrangement of the labral setae, and the lack of a procercus (Brundin, 1966). Orthocladiinae sp. C differs from the larva of Orthoclad. sp. c. from Pirongia in the formation of the labrum (SI is simple), and a procercus is present in the larva from Pirongia.

CHIRONOMINI

Larvae of 12 Chironomini taxa were recorded, either as fossils from the cores from Lakes Grasmere and Monowai, or from the surficial sediment samples from South Island lakes (see Table 5.1. and Table 8.5.). The identification of most Chironomini taxa did not present any difficulties using the key by Stark (1989). One undescribed taxon was recorded, Chironomini sp. A (Fig. I-A), which is described later. Morphological features of head capsules of the following Chironomini taxa are illustrated in Appendix I: Paucispinigera sp. a (Fig. V-G), Harrisius (Fig. V-J), Polypedilum (Fig. VIII-P), Parachironomus (Fig. VIII-Q), Xenochironomus (Fig. VIII-R), Cryptochironomus (Fig. VIII-S), Paucispinigera approximata (Fig. VIII-T), and Riethia (Fig.V-H).

All head capsules of Riethia (Fig. V-H), found as fossils, had been broken in halves. They have been identified by the characteristic ventromental plates which are almost in contact medially (Wiederholm, 1983), and the reduced size of the 2nd of the 6 pairs of lateral teeth. Adult males of one species, Riethia zeylandica, Freeman (1959), are described from New Zealand (Cranston & Martin, 1989).

The subgenus Polypedilum (Fig. VIII-P) of the genus Polypedilum is represented in New Zealand by 10 described species (Cranston & Martin, 1989). As larvae of this subgenus can not be differentiated to species level, it is not known which species of Polypedilum occurred in the past in Lake Grasmere. Stark (1981) found adult midges of P. pavidus and P. canum in light-traps and hand-collections from the shore of Lake Grasmere.

Fossil head capsules of Harrisius (Fig. V-J), possibly H. pallidus (Freeman, 1959), have been found only in core samples from Lake Monowai.

Cryptochironomus (Fig. VIII-S) has not as yet been described from New Zealand, but larvae with the characteristic mentum of this genus with a broad pale median tooth and 6 pairs of obliquely arranged, dark lateral teeth, have been recorded from Waitomo Stream and Lake Taupo (Forsyth & McCallum, 1981), and single head capsules have been found in the core from Lake Grasmere, and in surficial sediment samples from

Lakes Haupiri and Brunner.

Paucispinigera approximata (Fig. VIII-T) (Freeman, 1959) and P. sp. a (Fig. V-G) are endemic to New Zealand (Cranston & Martin, 1989). Head capsules of these species have been found as fossils in Lake Grasmere (Fig. 5.2) and in surficial sediment samples from several lakes in the South Island (Fig. 8.4.).

Only one species per genus has been recorded from New Zealand for Parachironomus (P. cylindricus (Freeman, 1959)), Xenochironomus (X. canterburyensis (Freeman, 1959), an obligate commensal of the freshwater mussel (Hydriella menziesi) (Forsyth, 1979; Forsyth & McCallum, 1978)), Cladopelma (C. curtivalva (Freeman, 1959; Forsyth, 1971)), and Kiefferulus (K. opalensis (Forsyth, 1975)). Head capsules of these taxa have been encountered as fossils in core samples from Lake Grasmere and surficial sediment samples from several South Island lakes, except for K. opalensis which occurred only in surficial sediments from Lakes Rotoiti and Rotorua near Kaikoura (Fig. 8.4.).

Head capsules belonging to Chironomus were common in most samples studied. There are four described species from New Zealand, two of those (C. antipodensis and C. subantarcticus) recorded only from the subantarctic islands of New Zealand (Sublette & Wirth, 1980). C. zealandicus has been recorded from a variety of freshwater habitats in New Zealand (see Stark, 1989), but these records may include C. analis because larvae of the two species are not distinguishable morphologically. Chironomus sp. a (Forsyth, 1971, 1978) is considered to be the "salinarius" form of C. zealandicus. It was not attempted in this thesis to differentiate the fossil Chironomus material.

Chironomini sp. A head capsules (Fig. Fig. I-A) have been found as fossils in surficial sediment samples in nearly all South Island lakes studied (Fig. 8.4.), and in core samples from Lakes Grasmere, Taylor, Monowai, and Blue Lake in Australia. One living larva has been collected from Lake Grasmere.

The characteristic features are : *the larva is 2.1 mm long; body and head capsule pale yellow; parapods bearing simple claws; lateral and ventral tubules absent; procercus absent; 6 anal setae arranged in a*

row. Head capsule with 2 pairs of eyes. Mentum with one median tooth and 7 pairs of lateral teeth, the first two pairs of laterals being of the same length; the remaining lateral teeth decreasing in size laterally; median teeth set forward of rest of mentum, in contact with the anteriorly produced inner ends of the ventromental plates between the second and third lateral teeth. Ventromental plates 3x as long as wide; anterior margin strongly crenulated, striation only weakly developed. Seta submenti short and simple. SI of the labrum pectinate, SII a very robust blade, twice the length of SI, SIII short and simple, SIV normal; labral lamella absent; pecten epipharyngis formed of 17 long teeth in a single series; premandible with 2 apical teeth, and 1 inner tooth, well developed brush present. Mandible with pale dorsal tooth, apical tooth and 3 inner teeth present; seta subdentalis simple, reaching up to the first inner tooth. Pecten mandibularis absent. Sensillum minusculum situated ventrolaterally on mandible forming a row with 2 external setae, of which the second is twice the length of the first. Antenna 5-segmented, basal segment shorter than segment 2, segment 4 slightly longer than segment 3; small Lauterborn organs present on segment 2; ring organ in basal 1/2 of first segment; blade shorter than flagellum, accessory blade 1/2 the length of blade.

Several morphological features of Chironomini sp. A indicate that this taxon may represent only an earlier instar of a Chironomini species, possibly the larvula of Chironomus as described by Mozley (1979). These characters are: the weak stratification and crenulation of the anterior margin of the ventromental plates, the short basal segment of the antenna, and the pecten epipharyngis consisting of long teeth (Sublette & Sublette, 1973). All these characters change in later instars of Chironomus, as well as the insertion of the ventromental plates into the mentum. This is obvious in the larvula but in fourth instar larvae the inner ends of the plates have turned posteriad. Fossil head capsules of Chironomini sp. A are usually well preserved. Head capsules of larvulae are rarely present in the fossil record. Iovino (1975) suggested that this is partly due to the complete liquefaction of the procuticle by the larva prior to ecdysis, leaving only the less durable thin non-chitinous epicuticular exuviae. If Chironomini sp. A were indeed the larvulae of Chironomus, fossil head capsules would have been derived from intact head caspules of dead larvae which contain both chitin and sclerotin.

As larvulae of Chironomus are not known in New Zealand or Australia, more taxonomic studies need to be carried out to verify the status of Chironomini A.

TANYTARSINI

Five taxa of Tanytarsini could be distingished in the fossil material and in recent collections.

Tanytarsus vespertinus and Tanytarsus funebris have been identified according to Stark (1989). T. funebris (Fig. VIII-U) can be differentiated from T. vespertinus by the median tooth of the mentum, which is lighter than the 5 pairs of laterals and displays lateral notching.

Corynocera (Fig. VIII- W,X) possesses the distinctive mentum and mandible similar to members of this genus described from the northern hemisphere (Anderson, 1943; Hirvenoja, 1961; Lehmann, 1973; Hofmann, 1971b, 1984; Walker & Mathewes, 1988). Corynocera head capsules have been found as fossils in Lake Grasmere and Lake Taylor (Schakau, 1986), and in surficial sediment samples from several lakes in the South Island (Fig. 8.4.), as well as one living larva from Lake Letitia. Corynocera from the South Island appears to belong to the ambigua group (Corynocera ambigua, Zetterstedt) but the mentum differs slightly from that described for C. ambigua from the northern hemisphere. In all South Island material studied, the three central teeth of the mentum form a distinct group and are clearly divided from the lateral teeth but not equal in height, the median tooth being always shorter than the two outer teeth; two pairs of lateral teeth are always present. Seven mental teeth are also present in Corynocera (described as Dryadotanytarsus duffi by Deevey, 1955), from the Pyramid valley deposits, South Island.

Paratanytarsus (Fig. VIII-V) can be separated from other Tanytarsini taxa by the bifid premandible, and the relatively strongly arched mentum with a median tooth, which has basal lateral notches, by the pecten epipharyngis consisting of 4 finger-like lobes, and short pedicellate Lauterborn organs (the latter two morphological characters

were never present in fossil head capsules). One species, Paratanytarsus agameta (Forsyth, 1971), is recorded from New Zealand, but is now considered to be the almost cosmopolitan P. grimmii (Langton & Cranston, 1988).

Head capsules of Stempellina (Fig. V-I) occurred only in core samples from Lake Monowai. This genus has not as yet been recorded from New Zealand, but two species (S. australiensis, Freemann, 1961; and S. johni, Glover, 1973) have been described from Australia. Larvae of Stempellina are easily distinguished from those of other Tanytarsini genera by the large, palmate apical expansion, which occurs on the antennal pedestal. The mentum has one pale, rounded median tooth and 6 pairs of darker lateral teeth; the ventromental plates are fan-shaped and separated medially. These characters are recognizable in the fossil head capsules from Lake Monowai, and therefore this taxon has been designated as Stempellina.

4.2. Conclusion

In summary, it has been shown that the taxonomy of the New Zealand Chironomidae is still far from being complete. Although the taxonomic status of the subgroups Chironomini and Tanytarsini is relatively well known, more taxonomic work needs to be carried out on taxa in the subfamilies Tanypodinae, Orthocladiinae, and Diamesinae. This work should include the rearing of adults individually from eggs or larvae so that larval and pupal stages can be associated with already described adults and that all life-history stages can be included in new descriptions. The latter point is important when designating new genera (Boothroyd, 1988) which should only be erected when unique features of a single stage can be confirmed by apomorphic features of other stages as recommended by Cranston and Oliver (1987).

CHAPTER V

CHIRONOMID ANALYSIS

5.1. Introduction

The analysis of fossil Chironomidae constituted the major part of the palaeolimnological studies on sediments from Lake Grasmere. Fossil remains in lake sediments document chronologically the faunal assemblages of past lake stages and the community succession through time. This study had two objectives: to follow the development of the fossil chironomid fauna through the last 6000 years of Lake Grasmere's history and to attempt to infer past environmental conditions of the lake and its catchment from the composition of the fossil chironomid fauna.

5.2. Results

The chironomid analysis was based on 56 sediment samples, each consisting of 1 ml of sediment. For the analysis, absolute numbers of chironomid head capsules per volume unit were counted (see Chapter 2.2.). A total of 5290 head capsules was retrieved averaging 96 head capsules per ml of sediment. The abundance of chironomid remains in the core fluctuated considerably (Fig. 5.1.). These fluctuations could be correlated partly with changes in the stratigraphy of the core. Layers of highly minerogenic sediment contained the lowest numbers of remains, whereas two peaks of greater abundances were found in the sections of the core with the highest proportion of organic matter. The greatest maximum abundance, at the 150 cm level, was not related to any special sediment features except for a relatively high content of water in this sample.

5.2.1. Numbers of Fossil Head Capsules

The sample at the base of the core (326 cm) contained neither fossil midges nor Cladocera, or plant remains. In the sample at the top of

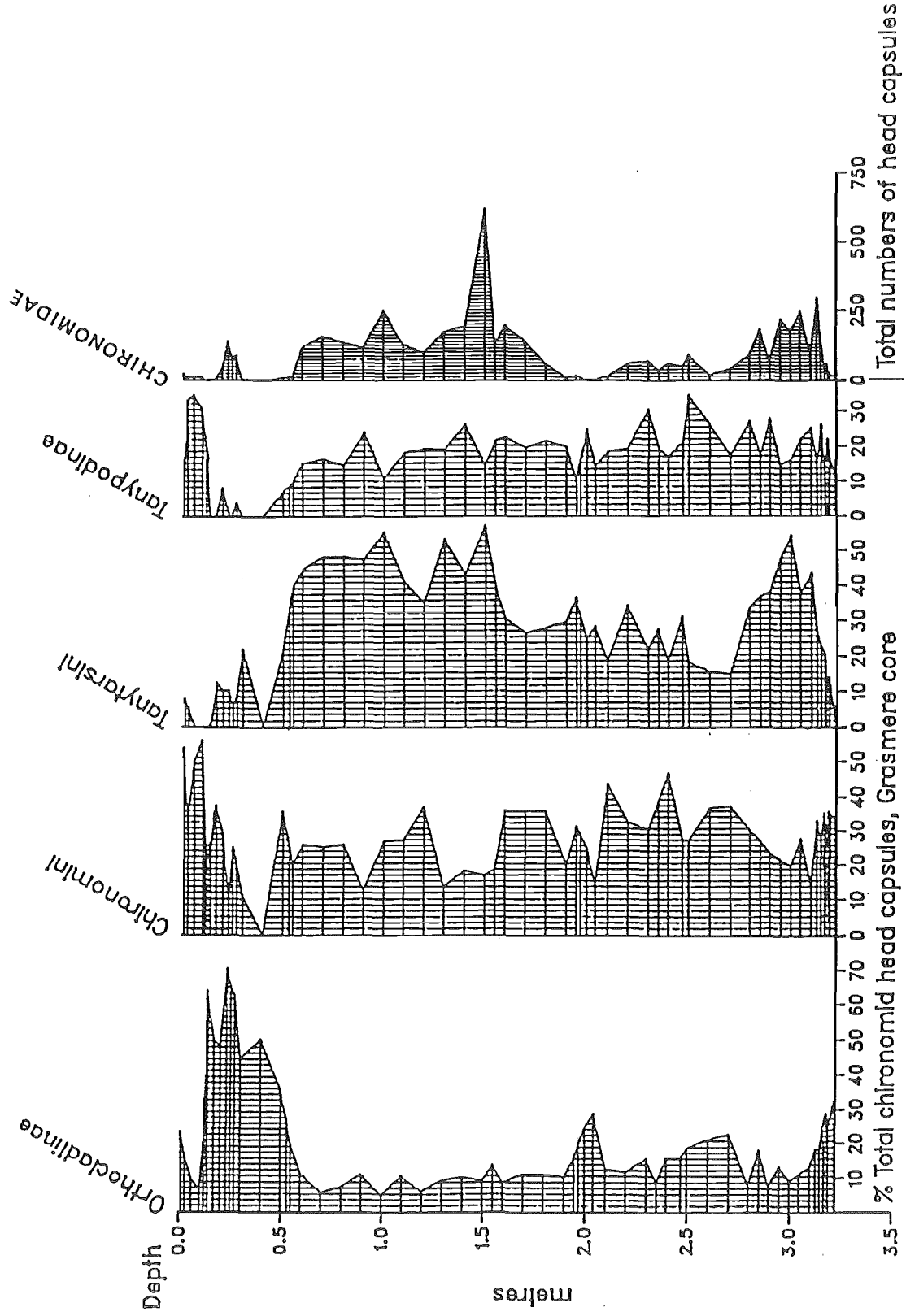


Fig. 5.1. Lake Grasmere: Total number of chironomid remains and the relative abundance (% of fossil sum at each sampling level) of the main chironomid subgroups in the samples from the core.

the clay/silt layer (322 cm) the first fossil chironomids were found in low numbers (Fig. 5.1.). After the change of sediment to organic clay gyttja, at 319 cm (Fig. 3.3.), numbers of head capsules in the samples rose quickly to the first maximum of abundance between 315 and 285 cm. Numbers of remains then decreased to a minimum at 260 cm, then rose slightly, and declined again to very low numbers between 210 and 196 cm. This part of the core contained the Grana minora sediment layer. The abundance of chironomids then increased in the following deposits of the core. In the 150 cm sample, 626 head capsules were counted which is an exceptionally high number of chironomid fossils to be found in this type of sediment. Numbers remained relatively high up to the 60 cm level. A sharp decline in the number of chironomid remains was found above the 60 cm horizon. The lowest number of head capsules occurred at the 40 cm level where only two head capsules were isolated. Generally, the youngest sediments contained only low numbers of midge remains in the samples, except for the organically rich layer in the top sediments (22-30 cm) in which numbers rose to a smaller third maximum in the core. A very low number of remains was found in the 12 cm sample (five head capsules). Above that horizon numbers of chironomid remains increased again slightly towards the top of the core.

5.2.2. Stratigraphy of the Chironomidae Subgroups

Five chironomid subfamilies occurred in the Lake Grasmere core. In the subfamily Heptagyini, only six head capsules were found, belonging to Maoridiamesa and the undescribed genus nr. Limaya. Four Podonominae head capsules occurred which belonged to Parochlus and Podonomus. All four genera are found in low numbers in streams in the Cass area today (Table 5.1. and see Appendix, Table II.3.).

Tanytarsini were the most abundant subgroup with a relative abundance of 37.3%, Chironomini were the sub-dominant group with 25.5%, Tanypodinae occurred with 17.9%, and Orthocladiinae with 15.8% relative abundance (Table 5.1.).

Comparing the relative abundance of the four main chironomid subgroups (Fig. 5.1.) it is clearly shown that Tanytarsini represented the

dominant group in the fossil chironomid fauna during most of the lake's developmental history under study. High relative abundances of Tanytarsini were found in the older sediments of the core (310-280 cm) and in the sediments between 160 and 60 cm. In the more recent sediments, from 50 cm to the top of the core, the Tanytarsini were no longer the dominant subgroup. A relatively low occurence of Tanytarsini was found in the sediment layers between 270 and 260 cm.

Orthocladiinae occurred throughout the core mostly with a relatively stable percentage (Fig. 5.1.). This subfamily had two slight maxima in abundance, one at the bottom of the core and the other in the samples derived from the sandy layer (204-200 cm). Orthocladiinae showed a peak in relative abundance in the younger sediments between 30 and 10 cm. The 50% relative abundance at the 40 cm level is meaningless because only two chironomid head capsules were found in this sample. One head capsule belonged to Orthocladiinae sp. IX, the other one was too fragmented to be identified.

Chironomini were present in relatively large numbers throughout the core but their percentage distribution showed distinct fluctuations. This subgroup was dominant in the sediments from 280 to 160 cm and in the bottom sediments of the core. No Chironomini head capsules were found in the 40 cm sample but above this sediment horizon, Chironomini occurred with increasing abundance and became the dominant element in the fauna in the uppermost samples in the core (Fig. 5.1.).

The relative abundance of Tanypodinae remained stable in most samples. A slight peak in abundance was found in the 247 cm sample and the youngest sediment layers. In the more recent sediments between 55 and 14 cm, Tanypodinae head capsules were not found or occurred in very low numbers (Fig. 5.1.).

5.2.3. Numbers of Chironomidae Taxa

The fossil chironomid remains from Lake Grasmere could be separated into 35 taxa but only 14 taxa occurred with a relative abundance higher than 1% of the total number (Table 5.1.). The number of taxa in the sediment samples varied considerably from only one

Table 5.1. Lake Grasmere: Fossil Chironomid Taxa (N - Number of Head Capsules, % - Relative Abundance, Percent of Total Fossil Sum).

TAXON	N	%
Chironomus sp.	726	13.7
Cladopelma curtivalva (Kieffer, 1917)	216	4.1
Polypedilum sp.	184	3.5
Chironomini sp.A	100	1.9
Paucispinigera approximata (Freeman,1959)	99	1.9
Parachironomus cylindricus (Freeman,1959)	12	0.2
Xenochironomus canterburyensis (Freeman)	8	0.2
Riethia sp.	1	0.02
Paucispinigera sp.a	1	0.02
Cryptochironomus sp.	1	0.02
Corynocera sp.	1525	28.8
Paratanytarsus sp.	246	4.7
Tanytarsus vespertinus (Hutton, 1902)	172	3.3
T. funebris (Freeman, 1959)	30	0.6
Orthocladiinae sp. IX	373	7.1
Cricotopus sp.	246	4.7
Orthocladiinae sp. XV	54	1.0
Cricotopus sp. 25	39	0.7
Rheocricotopus sp.	35	0.7
Eukiefferiella claripennis gr.	7	0.5
Orthocladiinae sp. XIV	23	0.4
Orthocladiinae sp. V	11	0.2
Orthocladiinae sp. I	8	0.14
Matakiri sp.	3	0.06
Synorthocladius (?) sp.	2	0.04
Apsectrotanypus (?) sp.	493	9.3
Tanypodinae sp.I	148	2.8
Genus nr. *Pentaneura* sp.	78	1.5
Macropelopia sp.	47	0.9
Gressittius antarcticus (Hudson, 1892)	47	0.9
Ablabesmyia mala (Hutton, 1902)	3	0.06
Maoridiamesa sp.	3	0.06
Genus nr. *Limaya* sp.	3	0.06
Parochlus sp.	3	0.06
Podonomus sp.	1	0.02
Chironomini	1349	25.5
Tanytarsini	1973	37.3
Orthocladiinae	835	15.8
Tanypodinae	947	17.9
Heptagyini	6	0.1
Podonominae	4	0.08
Not ident.	176	3.3
Not ident. to taxon-level	322	6.1

species in the 40 cm sample to 23 taxa in the sample at the 313 cm horizon (Appendix, Table II.2.). Throughout the core, sediment layers with relatively high numbers of species in the samples alternated with sediment layers with a lower diversity of chironomid taxa. In the first sample to contain chironomid remains at the base of the core (322 cm) only four taxa were found. In the following sediment layers, the species number increased and remained high up to the 280 cm level. Between 318 and 280 cm, an average of 18 species per sample was distinguished. These sediments had the highest chironomid diversity in the core. Above the 280 cm level, in the sediments between 270 and 220 cm, the species number ranged from 10 to 19 taxa in the samples with an average of 14 species per sample. The next layer (210 to 190 cm) had a low species diversity with a range of four to seven species and an average of 5 species per sample. Between 180 cm and 60 cm, the chironomid diversity increased again and the sediment samples contained an average of 16 taxa (a range of 12 to 20 taxa). In the youngest sediments, from 55 cm to the top of the core, a low species number was recorded. Species numbers in these samples ranged from one to 12 species, with an average of seven taxa per sample (Appendix, Table II.1).

Chironomini and Orthocladiinae were the most diverse subgroups with 11 taxa in the Orthocladiinae and 10 taxa in the Chironomimi (Table 5.1.). Except for one taxon, Chironomini sp.A, all Chironomini taxa could be identified to generic level (see Chapter IV). Five taxa of the Chironomini occurred with a relative abundance >1%. Chironomus sp. (13.7%), Cladopelma curtivalva (4.1%), Polypedilum sp. (3.5%), Chironomini sp. A (1.9%), and Paucispinigera approximata (1.9%) were the most abundant. Parachironomus cylindricus and Xenochironomus canterburyensis were rare and only one head capsule was found from three taxa, Riethia sp., Paucispinigera sp. a, and Cryptochironomus sp. These head capsules were found in the older sediments of the core (Appendix, Table II.3.).

The number of undescribed taxa in the Orthocladiinae was high (five taxa) due to the poor taxonomic knowledge of this group in New Zealand. Only three orthoclad taxa occurred with an abundance of more than 1% of the total fossils. These were: Orthocladiinae sp. IX (7.1%), Cricotopus sp. (4.7%), and Orthocladiinae sp. XV (1.0%). The

uncommon orthoclad taxa included Cricotopus sp. 25, Rheocricotopus sp., Orthocladiinae sp. XIV, and Orthocladiinae sp. V. The lowest number of head capsules was found for Orthocladiinae sp. I, Eukiefferiella claripennis, Matakiri sp., and nr. Synorthocladius sp.

In the Tanytarsini, only four taxa could be distinguished. Corynocera sp. was the dominant chironomid with 28.8% relative abundance. Besides Corynocera sp., Paratanytarsus sp. (4.7%), and Tanytarsus vespertinus (3.5%) were relatively abundant.

The most abundant Tanypodinae head capsules belonged to Apsectrotanypus sp. Two undescribed Tanypodinae genera occurred in quite large numbers, Tanypodinae sp.I and nr. Pentaneura sp. Three tanypod taxa occurred with a relative abundance < 1%: Macropelopia sp., Gressittius antarcticus, and Ablabesmyia mala.

5.2.4. Stratigraphy of Chironomidae Taxa

The temporal distribution of the 14 main chironomid taxa in the Lake Grasmere core showed some significant trends (Fig. 5.2.). The dominant taxon, Corynocera, appeared in a low relative abundance in the top sample of the clay/silt layer and became the dominant form in most sediment samples from 310 cm up to the 55 cm level. In the youngest sediments (50 cm to the top of the core), only one head capsule of Corynocera was found. Two samples derived from the sandy layer in the core (200 and 204 cm) did not contain any Corynocera head capsules and the abundance of the taxon at 260 cm was comparatively low.

Of the other Tanytarsini, Paratanytarsus was found in most samples throughout the core with a relative abundance of <10%, but this taxon had several isolated peak occurrences. In the two samples derived from the sandy layer in the core (200 and 204 cm), and in the 55 cm sample, Paratanytarsus was the dominant chironomid in the fauna. This dominance was not caused by any increase in numbers of head capsules of this taxon but by a marked decrease in the number of head capsules of most other taxa.

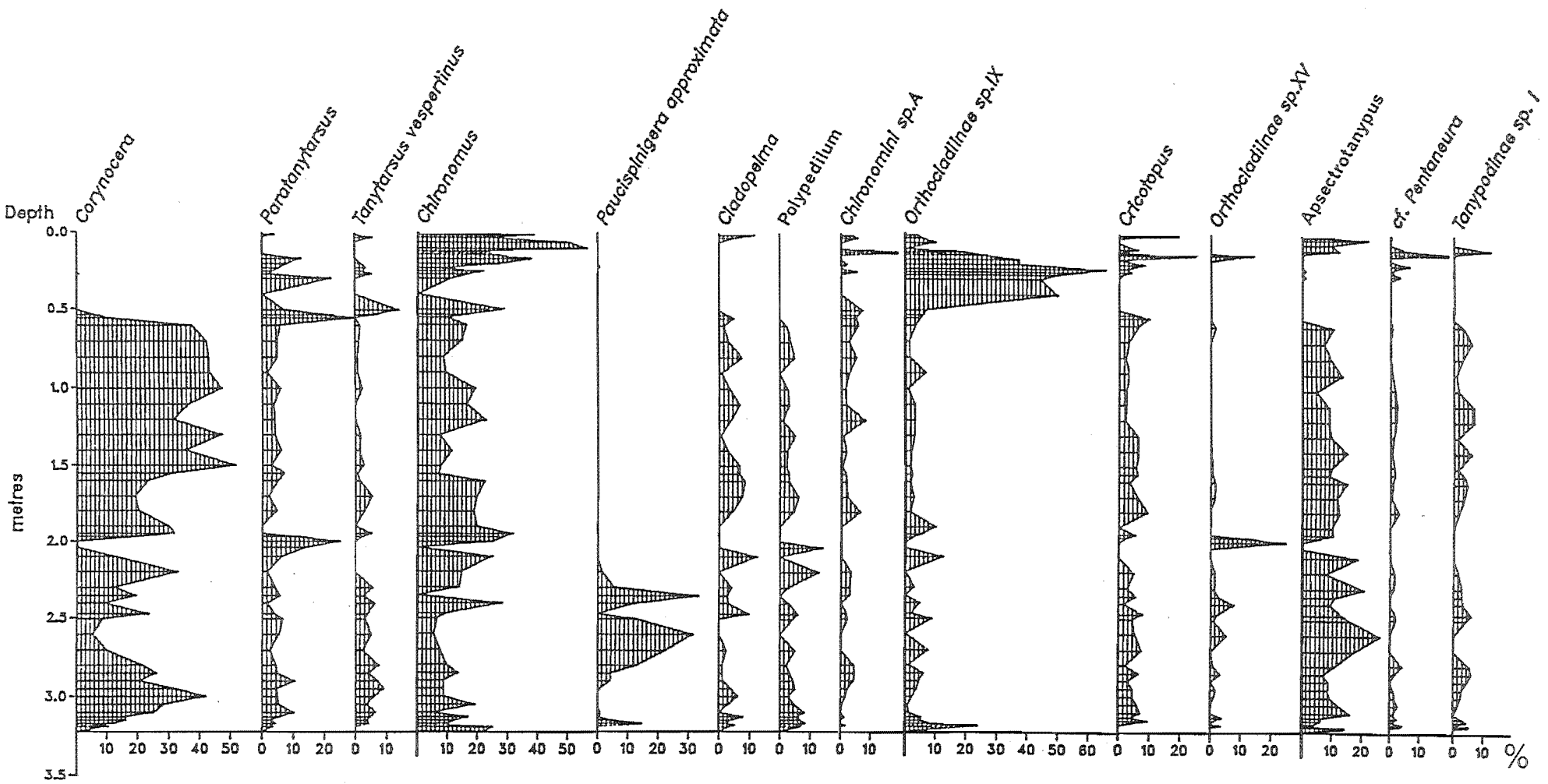


Fig. 5.2. Percentage diagram of the most abundant chironomid taxa for Lake Grasmere (percentages are calculated as proportions of all chironomid head capsules in each sample).

Tanytarsus vespertinus was not a common taxon in the fossil chironomid fauna of Lake Grasmere. This taxon had slightly higher abundances in the older sediments of the core between 318 and 230 cm.

The abundance of Chironomus in the core fluctuated strongly but the taxon was an important part of the fauna in nearly every sample. Chironomus head capsules were absent only in three samples (40, 204 and 235 cm). A pronounced peak in relative abundance of Chironomus occurred in the youngest sediments of the core.

Paucispinigera approximata appeared only in the older sediments of the core between 318 and 220 cm. This species was one of the dominant chironomids of the chironomid fauna during a period between 5000 and 3400 years ago.

Cladopelma and Polypedilum had very similar distributions throughout the core. Polypedilum disappeared entirely above the 60 cm horizon, whereas Cladopelma disappeared above the 55 cm level in the core. This latter taxon occurred again in the uppermost sediments of the core.

Chironomini sp. A was found with only low relative abundances in the core. A peak abundance of this taxon occurred at the 12 cm level. This was due to very low numbers of chironomid head capsules and taxa in this sample.

Orthocladiinae sp. IX occurred during the entire period covered by the core mostly in relatively low abundances but became the dominant chironomid taxon in the sediments between 40 and 12 cm. In the samples at the 23 cm level, 65.5% of all head capsules found belonged to this taxon. The maximum abundance of this orthoclad occurred during the time of the deposition of the organically rich layer in the upper part of the core (see Fig. 3.3.).

Head capsules of Cricotopus were present in most samples from the core. This taxon appeared first at the 317 cm horizon but was not found in samples from the sandy layer (200, 204 and 210 cm) and in several samples above the 55 cm level. Peak abundances of Cricotopus were noted at 14 cm and in the most recent sediments.

Orthocladiinae sp. XV generally occurred in low abundances throughout the older sediments of the core but was hardly found above the 140 cm level. The distribution of this taxon showed two single peaks of relative abundance, at the 200 and 14 cm horizon. These peaks were caused by the low number of head capsules and taxa in these samples.

The distribution of Apsectrotanypus in the core was relatively stable except for a small maximum at 270 cm. Head capsules of this taxon have not been found at the 204-200 cm level and in most samples between 55 and 12 cm in the core.

Nr. Pentaneura was not common in the fossil chironomid fauna from Lake Grasmere, although it appeared in low numbers in the basal sediments of the core. This taxon had its maximum abundance in the younger sediments.

Tanypodinae sp. I mostly occurred throughout the core but was absent in the sediment layers around the 260 cm and 200 cm horizon and disappeared above the 60 cm horizon. It was found again only in one sample (10 cm) in the younger sediments.

The distribution of the taxa occurring with less than 1% of the total fossils has not been shown graphically but some of these rare taxa were relatively abundant in individual samples. Rheocricotopus sp. occurred with a relative abundance of 11.7% in the 27 cm sample and 6.8% in the 25 cm sample. Eukiefferiella claripennis had a maximum abundance in the 50 cm sample (28.6% relative abundance), and Macropelopia sp. was more common in the oldest sediments. Between 319 and 315 cm this taxon had relative abundances of 3.6 to 6.3%. The taxon almost disappeared from the fossil fauna above the 285 cm horizon (Appendix, Table II.3). In the oldest sediments of the core which contained fossil remains of chironomids (322 cm), Cricotopus sp. 25 occurred with a relative abundance of 33.3%. In this sample the sole head capsule of Paucispinigera sp.a was found and one of the three identified head capsules of Ablabesmyia.

To summarize, 35 chironomid taxa were distinguished in the fossil chironomid fauna from Lake Grasmere. The fauna was clearly dominated by five taxa which had maxima of abundance during different periods of

the lake's history during the last 6000 years. These taxa were Corynocera sp., Orthocladiinae sp. IX, Chironomus sp., Apsectrotanypus sp., and in the older sediments Paucispinigera approximata.

5.2.5. Numerical Analyses

A hierarchical classification analysis was used to study the successive changes in the composition of the fossil faunal associations. The percentage similarity of community (PSc-index) was used as a similarity index. The classification was made as a group average clustering of the samples (see Chapter II).

The data matrix for all analyses consisted of the percentage abundance of 14 chironomid species in 55 samples. The sample at 326 cm was omitted from the analyses because this sample did not contain any fossil remains. Taxa which constituted less than 1% of the total fossil sum were excluded from the analyses. The original relative abundances of species, calculated as percentage of the total at each sampling level, were maintained for the analyses because the relative abundance reflects the numerical importance of a particular taxon in the fossil fauna.

The results of the classification analysis are shown in Fig. 5.3. Three main groupings of sediment sequences were formed:
Group I, 1-50 cm;
Group II, 60-110 cm, with samples 40 and 55 cm as a subgroup attached.
The third grouping (120-322 cm) consists of five subgroups:
Group III, 120-155 cm;
Group IV, 160-230 cm (with the 322 cm sample);
Group V, 240-280 cm;
Group VI, this group contains samples from several sediment layers:
220, 250 cm, and 310, 315, 317 cm;
and Group VII, 285-319 cm.

The samples at 290 and 300 cm form a subgroup of the combined Groups IV, VI, and VII. Three samples (23, 204, and 235 cm) were not placed into any of the groups. These samples are outliers and exhibit unusual features in the composition of the fossil chironomid fauna. The 40 and

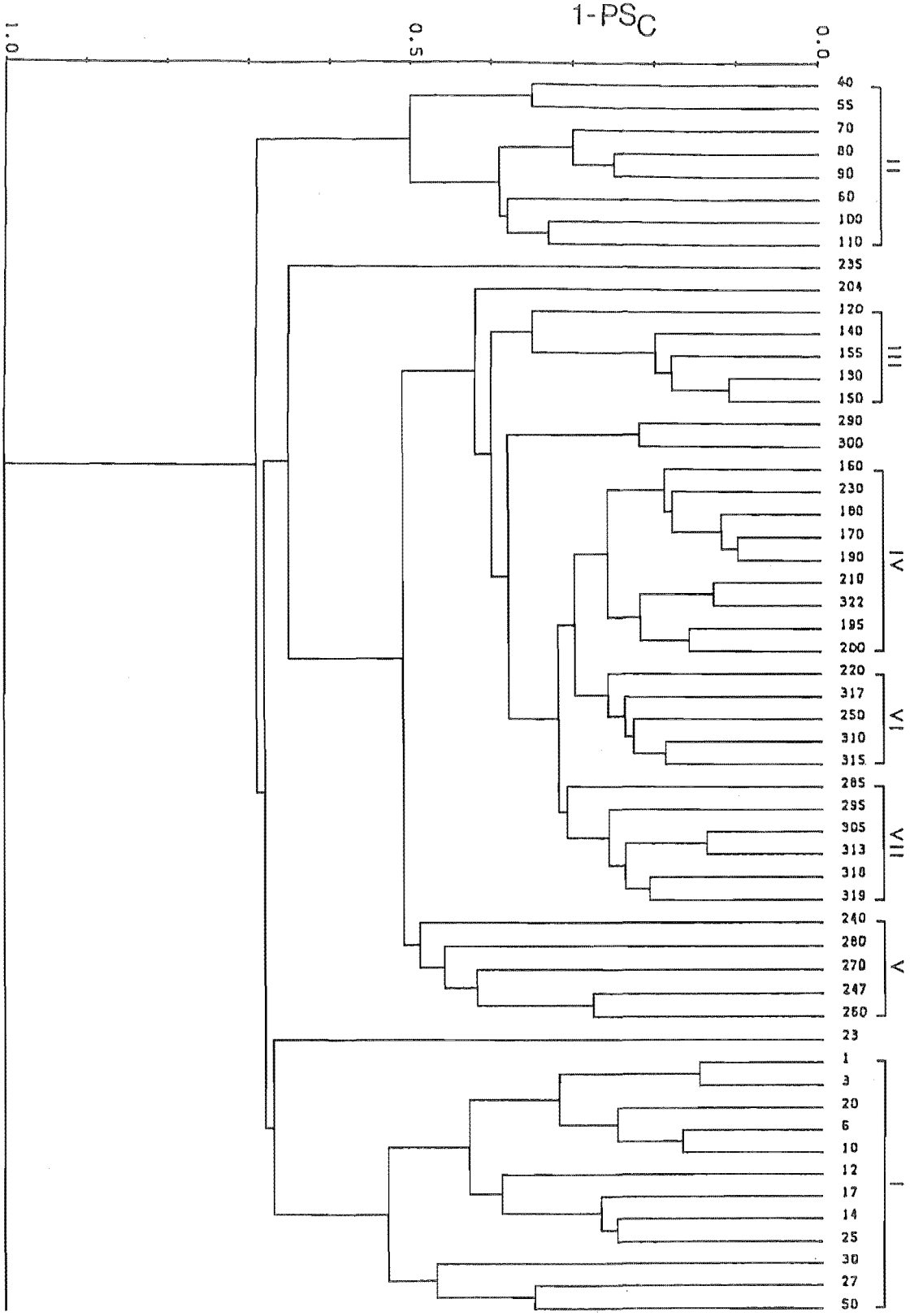


Fig. 5.3. Lake Grasmere: Dendrogram based on an average linkage cluster analysis on the relative abundance of the fossil chironomid taxa in the samples from the core. The vertical axis gives the values of the dissimilarity index. The group codes are indicated by Roman numerals.

55 cm samples also belong to this group of outliers. The sample at the 23 cm horizon is characterized by the highest percentage (65.5%) of Orthocladiinae sp. IX in the core, and the sample at 40 cm has Orthocladiinae sp. IX as the only faunal component (50 % relative abundance in a total of two specimens, the second head capsule found could not be identified). In the 55 cm sample, Paratanytarsus occurred with a relative abundance of 30%. The 204 cm sample is classified as an outlier because only Polypedilum (14.3%) and Orthocladiinae sp. XV (14.3.%) have been included in the analysis (the other species occurring at <1% relative abundance), and in the 235 cm sample the highest relative abundance of Paucispinigera approximata (33.3%) was found.

The results of the classification analysis indicate clear vertical changes in the composition of the fossil chironomid fauna in the core following the time series of the samples with Group I representing the youngest sediments and Group VII the oldest organic sediments. An exception is Group VI which contains samples corresponding to Group IV (220 cm), Group V (250 cm), and Group VII (310, 315, and 317 cm). Group VII represents the sediment layer which is most heterogenous because of the 11 samples collected from these sediments (285-319 cm), five samples are clustered into different groups.

In Table 5.2., the mean relative abundances (of all samples in one group) of the 14 chironomid taxa are given for each sample cluster. The basis for the division of sample clusters is clearly shown for most groups. Group I is characterized by the absence of Paucispinigera, Polypedilum, and Corynocera, the lowest proportion of Apsectrotanypus in the core, and the highest proportion of Chironomus and Orthocladiinae sp. IX. Group III and the closely grouped 290 and 300 cm samples exhibit very similar patterns of species proportions with low relative abundances of Chironomus and relatively high proportions of Corynocera. This relationship changes in Group IV in which Chironomus occurs with a high relative abundance, but that of Corynocera is lower, and the highest proportion of Apsectrotanypus was found. Group V has a lower proportion of Corynocera and Chironomus but the maximum occurrence of Paucispinigera in the core. In Group VI the abundance of Chironomus is at its lowest level in the core, but Polypedilum has a maximum occurrence. Group VII is characterized by

Table 5.2. Lake Grasmere: Two-way table of coincidence giving the mean relative abundances (%) of the fossil chironomid taxa in each sample cluster (Groups I - VII, and samples 290/300cm, N = number of samples per group).

TAXON/GROUP	I	II	III	290/300cm	IV	V	VI	VII
Chironomus	29.4	14.0	11.2	8.9	22.1	12.1	9.9	15.6
Paucispinigera	0.0	0.0	0.0	2.2	0.6	15.9	6.8	2.4
Polypedilum 0.0	2.8	2.8	3.4	1.9	3.2	8.1	5.2	
Cladopelma	1.4	3.9	4.2	3.8	4.2	3.3	1.3	4.2
Chironomini A	3.4	3.1	2.3	2.0	1.4	1.3	1.1	1.8
Corynocera	0.0	41.6	39.4	31.3	16.6	14.0	20.1	19.5
T. vespertinus	2.4	1.1	1.3	7.6.	2.3	5.1	3.7	3.9
Paratanytarsus	5.0	4.5	4.9	4.8	5.3	3.5	5.1	4.2
Orthocl. sp. IX	29.8	2.7	2.3	3.3	4.1	3.1	4.5	9.5
Cricotopus	5.5	3.3	5.2	3.7	3.0	4.9	5.5	3.0
Orthocl. sp. XV	1.0	0.6	0.4	0.6	3.3	3.2	1.0	2.0
Apsectrotanypus	4.5	9.1	10.5	9.2	21.5	15.6	10.2	8.2
Tanypod. sp. I	1.0	3.6	3.8	3.3	1.4	2.9	2.1	3.0
nr. *Pentaneura*	3.1	0.9	1.3	0.9	0.6	1.3	1.9	1.9
N	12	6	5	2	9	5	5	6

relatively high proportions of Corynocera and Chironomus and a low abundance of Apsectrotanypus.

However, there is one major irregularity which cannot be explained by the original data matrix and this concerns the separation of the samples of Groups II from all other samples in the core (Fig. 5.3.). The relative abundances of most species in Group II are very similar to those in Group III, except for slightly higher proportions of Chironomus and Corynocera in Group II.

According to Matthews et al. (1991) dendrograms derived by hierarchical clustering should be balanced. Balanced dendrograms indicate good clustering into roughly equal-sized clusters whereas unbalanced dendrograms indicate little real clustering, but a gradual accumulation of sample points into a single group. As the Lake Grasmere dendrogram is unbalanced in part (pertaining to the division of Group II from all other groups) this possibility of an artefact of the clustering method has to be taken into account. Matthews et al. (1991) also found that the tree development in hierarchical clustering was seriously affected by outliers. As described earlier, the data matrix of the Lake Grasmere fossil chironomids contained several outliers of which especially sample 40 cm (only containing two head capsules and therefore a 50% relative abundance of Orthocladiinae sp. IX) and sample 55 cm (the sole sample to contain as much as 33.3% of Paratanytarsus) could have caused the irregularity of the cluster dendrogram. For my interpretation of the development of the fossil chironomid fauna of Lake Grasmere, I have discarded the division between Groups II and III.

Although Matthews et al. (1991) found hierarchical clustering an unsatisfactory method of analysing limnological data, this method was used successfully to describe associations of Chironomidae in relationship to the benthic lake type system in Scandinavia (Wiederholm, 1981; Kansanen et al., 1984) and in the other investigations described in this study analysing fossil chironomids from Blue Lake, recently deposited chironomids in surficial samples from 32 lakes in the South Island, and fossil Cladocera from the Lake Grasmere core. Modifications could be made to hierarchical clustering to improve its use for chronological samples, e.g. the explicit removal of outliers from the data set (Matthews et al., 1991). In the context of ecological research, I regard 'outliers' as a potential sign of ecological change in the community caused by possible alterations of the environment, and therefore I am generally hesitant to omit outliers from statistical analyses when only a small number of samples is available for analysis, as is the case in this study.

The second approach in analysing species composition and structure was by using a correspondence analysis (reciprocal averaging) (Fig. 5.4.) on the relative abundance of the 14 abundant fossil

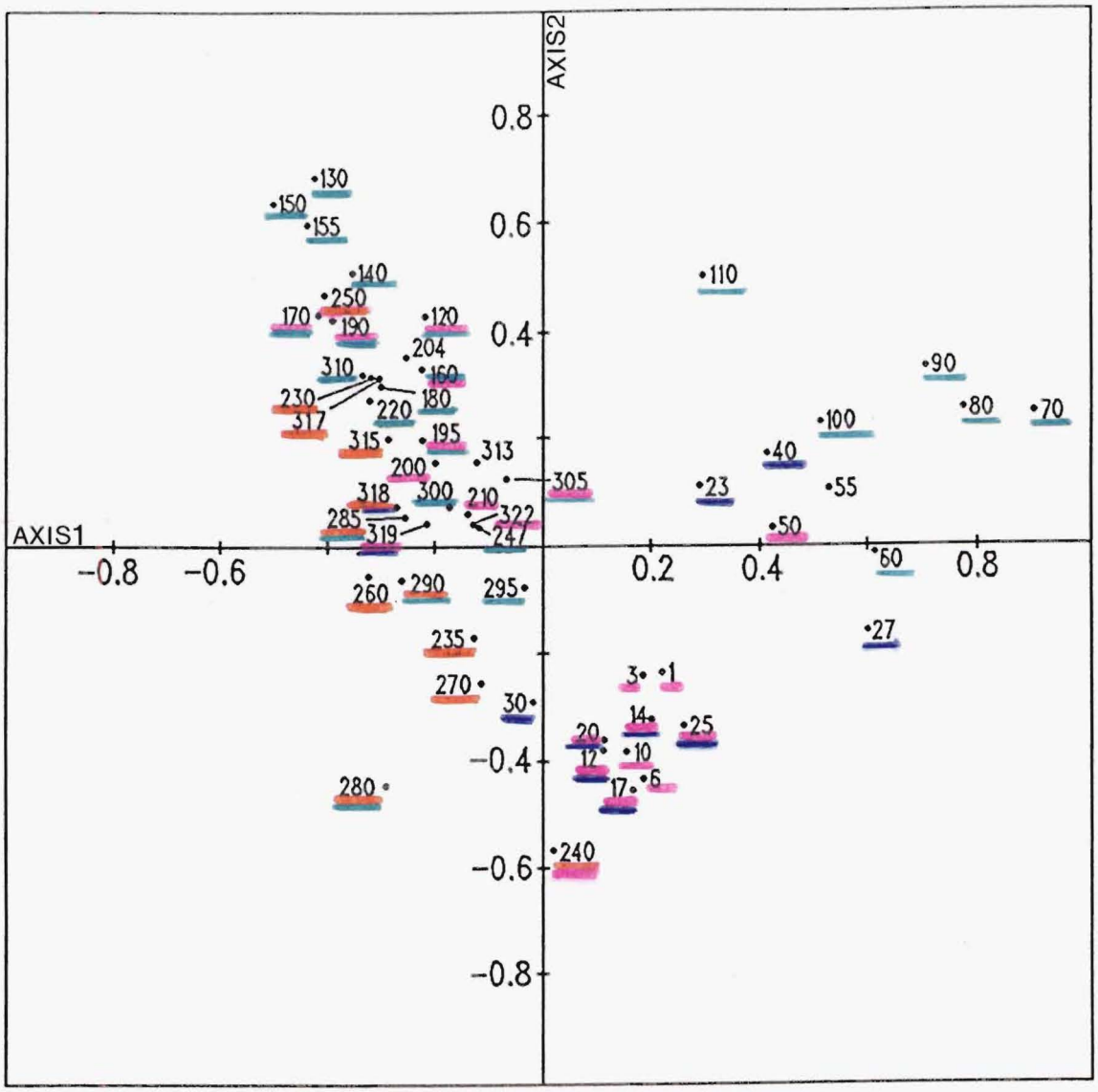


Fig. 5.4. Reciprocal averaging ordination of the samples from the Lake Grasmere core. The analysis is based on the relative abundance of fossil chironomid taxa in the samples. The colour code on the overlay denotes the dominant taxa in the samples: green - *Corynocera*, orange - *Paucispinigera approximata*, blue - Orthocladiinae sp. IX, pink - *Chironomus*.

chironomid taxa in 55 samples from the Lake Grasmere core. In reciprocal averaging (RA) analysis (=correspondence analysis), as well as in detrended correspondence analysis (DCA), the ecologically interpretable variability is usually explained within the first three axes, with the fourth and subsequent axes being uninterpretable (Gauch, 1982; Birks, 1985). The ordination diagram (Fig. 5.4.) represents the sample scores for the first two axes. The ordering of samples in RA is based on species scores (X) (and the ordering of species is based on sample scores (Y)). A measurement of the reliabilility of the species scores as ordering criteria is given by the canonical correlation R which is higher with higher reliability of the species scores (Orloci, 1978). In the present analysis, the canonical correlations are R(X/Y) = 0.5697 for Set 1, and R(X/Y) = 0.4649 for Set 2.

In the ordination diagram (Fig. 5.4.) the colour code denotes the dominance (or the presence in case of Paucispinigera approximata) of the main taxa in the samples. The ordination produced the same three main groupings as the cluster analysis: Group I (the youngest sediments) is characterized by the absence of Corynocera, and high abundances of Chironomus and Orthocladiinae sp. IX., Group II is characterized by a dominance of Corynocera, whereas samples of the third grouping (Groups III-VII) generally are characterized by relatively high abundances of either Corynocera and Chironomus, or Paucispinigera.

Correspondence analysis is known to produce frequently a 'horseshoe' configuration in the first two axes (Hill & Gauch, 1980; Jackson & Somers, 1991). It was suggested (Wartenberg et al., 1987) that this horseshoe effect occurs because sites "are considered similar due to the corresponding lack of individuals of most species, rather than the presence of members of the same species. This similarity leads to *involution*, the closeness (in species space) of dissimilar extremes of an environmental gradient". This 'horseshoe' effect can be seen in Fig. 5.4. Group I (dominated by Orthocladiinae sp. IX and Chironomus) is positioned closest to Group V, which contains samples with a relatively high abundance of Paucispinigera. Taking into account the 'horseshoe' effect, it can be seen in Fig. 5.4. that the samples are ordered following the time series of the samples in the core. The

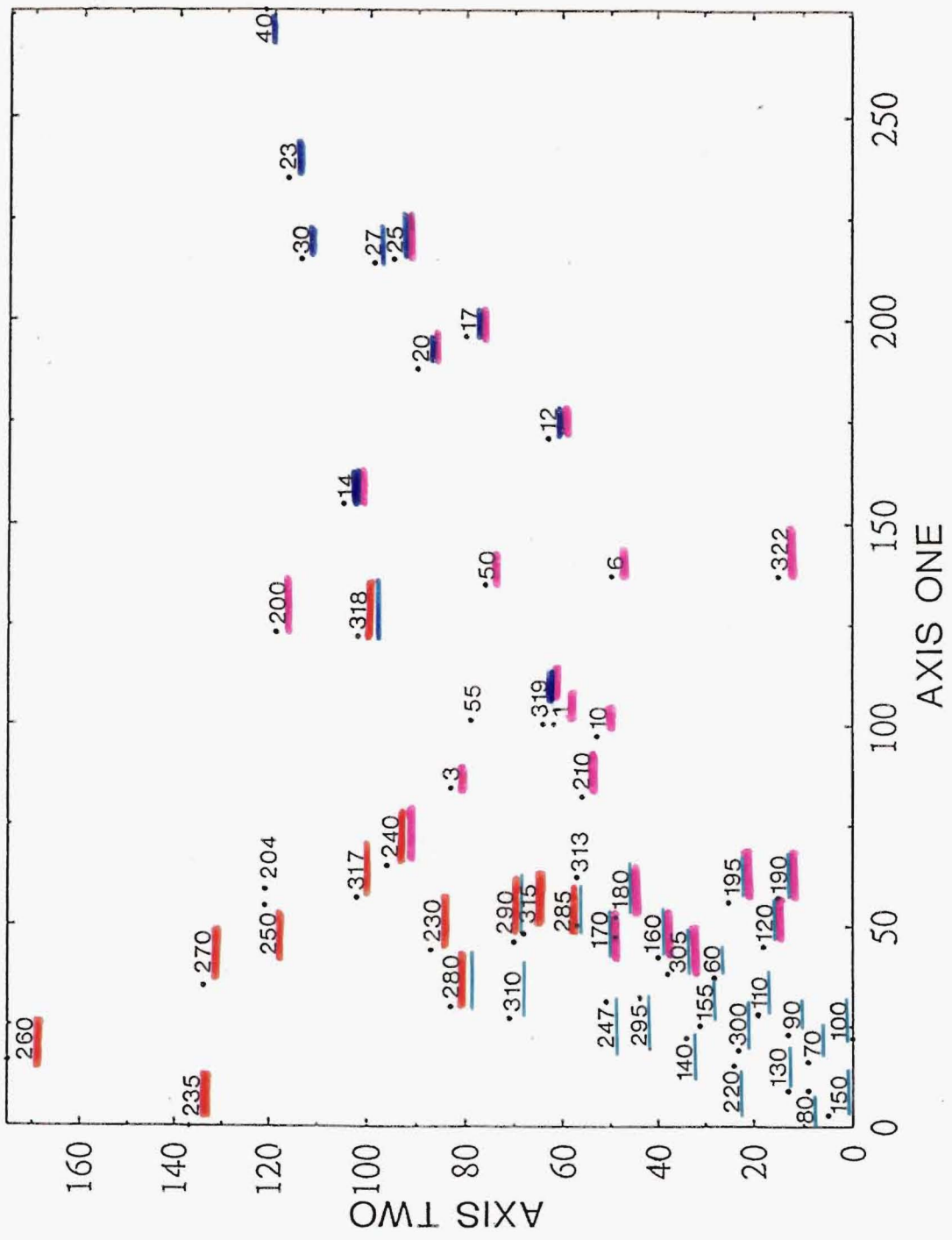


Fig. 5.5. Lake Grasmere: Detrended correspondence analysis of samples from the core based on the relative abundance of the fossil chironomid taxa in the samples. Colour code as in Fig. 5.4.

samples with the youngest sediments have low positive scores on axis one and negative scores on axis two; the samples of Group II (60-110 cm) have high scores on axis one and two; whereas samples of Groups III-VII have negative scores on axis one and decreasing scores on axis two. An exception are the samples dominated by Paucispinigera, which form the involution, with negative scores on both axes.

In order to test whether the 'horseshoe' effect was responsible for the resulting ordination, a detrended correspondence analysis (DCA) was carried out on the same data matrix (Hill & Gauch, 1980). DCA is a modification of the traditional correspondence analysis. The process of detrending (removal of the 'horseshoe' effect) is a forced adjustment of the site scores on the second axis and all subsequent axes so that no linear or low-order polynomial relationships remain with prior axes (Gauch, 1982). The ordination diagram produced by the DCA analysis (Fig. 5.5.) shows that the 'horseshoe' effect has disappeared but that the main trends of the previous ordination remain the same. Samples of Group I have high scores on axis one (especially samples which are dominated by Orthocladiinae sp. IX) whereas samples with high relative abundances of Corynocera (Groups II and III, and Groups VI and VII) have low scores on axis one. Samples which contain a high proportion of Paucispinigera have the highest scores on axis two (mainly Group V).

5.3. Discussion

The sediment core from Lake Grasmere covered the last 6000 years of the lake's developmental history. During this period, it appears that no major climatic change occurred as all sediments in the core were deposited during the Nothofagus phase of the Holocene. Therefore, it is unlikely that influences of macroclimate (e.g. a major change in temperature) would have been the cause of changes in the faunal composition of the fossil chironomids of Lake Grasmere.

Factors to which variations in the chironomid fauna might be attributed include the trophic state or the productivity of the lake, the oxygen concentration of the hypolimnion (Brundin, 1951; Hofmann, 1978, 1991; Wiederholm & Erikson, 1979), and the quality and

availability of food (Sæther, 1979; Kansanen et al, 1984; Warner & Hann, 1987). Hofmann (1983a) and Warwick (1980, 1989) emphasized the significance of sedimentation processes. Moore (1980) and Graham and Burns (1983) suggested that the production of benthic animals such as chironomids is linked to that of the phytoplankton through the sedimentation and resuspension of organic matter.

The interpretation of the observed changes in the fossil chironomid associations of Lake Grasmere presents some difficulties. Two factors restrict a detailed analysis of the faunal succession and its ecological significance: the relatively high number of undescribed or previously unknown taxa in the Lake Grasmere core (especially in the subfamilies Orthocladiinae and Tanypodinae); and the rather sparse ecological information available for many chironomid species in New Zealand. The ecological requirements of three of the 14 taxa which occurred with a relative abundance of more than 1% of the total fossil sum (Table 5.1.), Chironomini sp. A, Orthocladiinae sp. XV, and Tanypodinae sp. I, are not known at all. As described in Chapter IV, the taxonomic status of these taxa is uncertain, as Chironomini sp. A and Tanypodinae sp. I may be early instars of Chironomus and Apsectrotanypus respectively, and Orthocladiinae sp. XV may be the fossil form of Orthocladiinae C.

However, the existing ecological information about various present-day chironomid species whose fossils were found in the Lake Grasmere core, makes it possible to reconstruct some aspects of the lake's history. It appears that pronounced shifts in the structure of the chironomid community have been caused mainly by changes in the hydrology and the inflow to the lake and by variations in the rate and type of sedimentation. Changes in types of substrate and in lake productivity also had an influence on the fossil chironomid fauna.

The clay/silt layer at the base of the core represented a major environmental disturbance for the bottom fauna of the lake. The massive input of fine mineral sediments was carried into the lake by either Ribbonwood Creek (in which case the waters of the creek must have entered the lake as a surface inlet) or the Cass River, and must have caused high turbidity. The rapid mineral sediment accumulation appears to have eliminated the profundal fauna. The sample at the

bottom of the core consisted almost entirely of clay and silt particles.

The effects of sediment increase have been documented mainly for stream ecosystems in New Zealand (see Ryan, 1991). Suspended and deposited sediments affect the benthic community in several ways, e.g. interference with feeding which will lower benthic productivity (Graham, 1990); benthic densities may be reduced through death by smothering and an increase in the drift fauna; and the composition of benthic communities may be influenced by favouring predators and collector-browsers, such as the mayfly Deleatidium sp., over specific browsers or grazers. In the South Island unstable braided rivers which are affected regularly by floods causing bed load movement and increased suspended sediment loads are characterized by a low species diversity (Sagar, 1986). Flood magnitude and flood frequency appear to be important in limiting benthic invertebrate populations in the Rakaia River (Sagar, 1986). Similar effects of floods on benthic invertebrate populations have been recorded from other New Zealand streams and rivers. Pierce (1983) found that the species composition in the Cass River into Lake Tekapo was similar to that in the Rakaia River and that the invertebrate density was inversely related to preceding river discharge. Rivers with high loads of suspended sediment emptying into lakes will cause increased turbidity in the lake. This influx should affect the lake benthos in similar ways to the effect on stream benthos. A study of the distribution of benthic invertebrates along a natural turbidity gradient in Lake Temiskaming, Ontario-Quebec, (Sallenave & Barton, 1990) revealed that the numerical abundance of one of the most common invertebrates in the benthic fauna, the chironomid Heterotrissocladius oliveri, was negatively correlated with turbidity. The same trend was exhibited by other chironomids in the community, which increased in abundance with decreasing turbidity. The exception was Procladius, a facultative predator, whose distribution was not adversely affected by turbidity.

Several studies of South Island streams demonstrate a rapid recovery of the benthos from sediment-induced effects through refuge seeking behaviours, flexible life histories and effective recolonization mechanisms (Scrimgeour et al., 1988; Scrimgeour & Winterbourn, 1989). According to Luedtke et al. (1976) stream recovery depends upon two

factors: the elimination of the sediment source and the ability of the stream to flush out the deposited material. This may not be the case in a lake ecosystem as turnover times are longer.

The basal layer of the Lake Grasmere core was composed of silt and clay particles which have diameters of 0.06-0.002 mm (silt) and <0.002 mm (clay). Such fine sediment particles are highly mobile and may stay suspended in a lake for a long time (Ryan, 1991). Resuspension of fine sediment through wind and/or wave action is also possible in shallow lakes (Håkanson & Jansson, 1983) and could have extended the period of disturbance in shallow Lake Grasmere. It is not possible to determine the duration of the high sediment influx into Lake Grasmere as there is not enough organic material available for dating. It is also difficult to judge the timing of the recolonization of the chironomid fauna because a high sedimentation rate can dilute the apparent amount of fossil remains which are deposited.

During the last 6000 years of Lake Grasmere's history there have been five periods of increased mineral input. All of these had detrimental effects to various degrees on the fossil chironomid fauna. These periods are represented by the sediment layers: 326-320 cm, 270-260 cm, 210-200 cm, 55-30 cm, and 17-12 cm.

The first chironomid remains were found in the 322 cm sample. Initial numbers were low (9 head capsules/ml sediment) and the faunal components included only four taxa. The dominant chironomids were Cricotopus sp. 25 (33.3% relative abundance) and Chironomus (22% relative abundance). At present C. sp. 25 is an exclusively littoral form which was found living only on the pebbled south-eastern shore of the lake, presumably feeding on the filamentous algae which cover the pebbles (pers. obs.). Living larvae of Chironomus were found in littoral as well as profundal samples from Lake Grasmere. The single living larva of Paucispinigera sp. a, which was collected by the author, was obtained in a hand-net sweep sample from the shore of nearby Lake Lyndon (on 7 May, 1990) and Ablabesmyia mala was collected from the littoral of Lake Pearson, which is located adjacent to Lake Grasmere, by the author also on 7 May, 1990. The present-day occurrence of all four taxa in the littoral zone suggests that at the end of the period of on-going high turbidity chironomids either

recolonized the lake from the littoral or survived in an area of the littoral which was removed from the input source.

The change in sediment consistency to organic clay mud at the 319 cm level indicated the termination of the high sediment input followed by clearing lake waters. Numbers and diversity of chironomids increased rapidly in conjunction with a possible rise in lake productivity about 5500 years ago, as was indicated by the relatively high organic content of the sediments between 315 and 295 cm.

In the 319 cm sample, 28 head capsules belonging to 11 taxa were found. In the two following samples, 318 and 317 cm, the number of head capsules increased to 59 and 48 respectively, which could be differentiated into 15 taxa. A marked increase in the number of head capsules and chironomid taxa occurred at the 315 cm level, and the maximum number of taxa (23) and head capsules (296) in the oldest organically rich sediments of the core were recorded at the 313 cm level. By this time the content of organic matter had increased from 3.7% in the 322 cm sample to nearly 10% in the 313 cm sample (Appendix, Table II.1.). Numbers of remains and taxa remained high, corresponding to the relatively high content of organic matter in the sediments above the 313 cm horizon, and decreased abruptly after the decline in organic matter content between 295 cm (15.7% organic matter, the maximum values reached in the older sediments) and 290 cm (6.2% organic matter). All three parameters, number of chironomid head capsules and taxa and the content of organic matter, declined to low values at the 260 cm level (5.5% organic matter, 19 head capsules, 10 taxa). The correlation of organic matter content of the sediments and the numbers and diversity of chironomids shows the strong influence of the substrate type on chironomid communities (Warwick, 1980, 1989). Whereas the pronounced mineral sediment accumulation inhibited the growth of the chironomid community, the increased availability of organic food resources, as indicated by the increase in organic matter in the sediments after the decline of the mineral input, supported an increasingly numerous and diverse fauna during the period of higher lake productivity. The period of higher lake productivity came to an end abruptly between 295 and 290 cm where the content of organic matter declined considerably. This abrupt change in the deposition of organic matter might point to an allochthonously derived source of

nutrients which caused the temporary increase in lake productivity, and which stopped at some time after the 295 cm sediment horizon had been deposited.

An analogue for the temporary amplification of the productivity of Lake Grasmere ca. 5600 years ago may be found in the early phase of trophic upsurge which is experienced in recently filled reservoirs (Duthie, 1979; Han & Duthie, 1989). Productivity of a lake or reservoir, as indicated by changes in biomass and by changes in deposition of organic matter, is closely associated with changes in nutrient loading of a system (Vollenweider, 1971). Phosphorus is the limiting nutrient in most freshwater systems. In the case of newly flooded reservoirs, phosphorus is leached from inudated soils and vegetation. This phosphorus supply to the reservoir causes an increase in lake productivity, which will decrease again with the decline of phosphorus in the flooded terrestrial soil and vegetation, and will become a trophic depression (Duthie, 1979). A temporary supply of phosphorus to Lake Grasmere ca. 5600 years ago might have caused the relatively brief period of increased lake productivity, but the phosphorus would have been derived from a different source than submerged terrestrial vegetation and soil.

Bush et al. (1992) recorded high phosphorus concentrations in sediments from Lake La Yeguada, Panama, before 10,800 yr B.P. As the source of the nutrient input, Bush et al. (1992) identified runoff from the catchment, rich in slightly weathered clay particles which carried phosphate molecules adsorbed on the surface. The phosphate molecules became available for algal growth, which was shown by relatively high chlorophyll concentrations in the Pleistocene sediments. Climatic change around 10,800 yr B.P. in Panama was responsible for a change in the type of clay input thereby reducing the input of phosphorus to the system. In New Zealand, rivers can transport large silt loads to lakes (Pickrill & Irwin, 1983) and these silt loads can carry phosphate molecules sorbed on the surface of the suspensoids. Viner (1988) studied phosphorus associated with stream-borne particles in the Tongariro River, in the North Island, and showed that smaller particles carried proportionally more phosphorus and that this phosphorus was potentially available for plant growth. Although Viner (1988) did not quantify the available phosphorus

transported by river-suspended load, it is conceivable that greater magnitude floods which transport greater loads of particulate matter will also carry greater amounts of phosphorus. It is possible that the basal layer of the Lake Grasmere core, composed of clay and silt particles, provided the nutrient boost necessary for the period of relatively high lake productivity, in the form of phosphorus entering the lake sorbed on the surface of clay particles. Although the suspended clay and silt particles caused turbidity which suppressed plant growth and benthic development, the nutrient boost would have remained when the lake waters became clearer. Nutrients could have become available either through dissolution of phosphate or biological uptake, e.g. by bacteria or algae, which would transfer the originally adsorbed phosphorus into organic particulate phosphorus. Golterman (1977) showed that phosphate bound into the clay lattice was not available for algae, but that phosphate adsorbed onto clay particles could be utilized by algae in cultures. This nutrient increase therefore could have provided the conditions for the increase in lake productivity. The nutrient supply was limited as was shown by the marked decrease of organic matter between 295 and 290 cm and corresponding decline in numbers of chironomid remains.

It appears that the basal clay and silt layer was derived from a source beyond the boundaries of Lake Grasmere's more recent catchment because during some later stages in the development of the lake when mineral matter deposition was intensified a significant increase in organic matter was not shown, and the lake remained relatively unproductive until anthropogenic activities increased the nutrient supply to the lake. This supports the suggestion that the sediments constituting the basal layer were transported to the lake after a high magnitude flood by an inflowing river, possibly the Cass River, which might have flowed into the lake 6000 years ago.

In the chironomid community, originally dominated by Cricotopus sp. 25 (322 cm) and Chironomus at 322 and 319 cm, a shift in dominance occurred to a fauna dominated by Orthocladiinae sp. IX at 318 and 317 cm. In the following sediment layers Corynocera became the dominant taxon, but the chironomid assemblage had several abundant species. Chironomus and Apsectrotanypus were abundant, and Paucispinigera approximata was present. This sediment sequence (319 to

295 cm) is represented in the cluster analysis partly by Group VII, partly by Group VI and the separately clustered 290/300 cm samples (Fig. 5.3., Table 5.2.). Table 5.2. shows the trends in the development of the faunal composition in these sediment sequences: the abundances of Corynocera and Apsectrotanypus and P. approximata were increasing, whereas the abundance of Chironomus was decreasing from the older sediments upwards in the core.

According to the diatom stratigraphy (see Chapter III, section 3.8.) the lake during this period was shallow (possibly 3-5 m deep) and macrophytes were abundant, as shown by the dominance of the epiphytic Fragilaria species. The lake during this time supported only a moderate littoral diatom fauna (Fig. 3.4.) without indicator species of eutrophic waters. Based on the fossil diatom flora of this period, it appears that the increase in lake productivity would not have been marked, e.g. changing the trophic state of the lake to mesotrophy or even eutrophy. But the organic matter content of the sediment between 315 and 295 cm was considerably higher than in the earlier and most subsequent lake phases and the productivity in the lake was high enough to support the most diverse, but not the most numerous, chironomid fauna in the core during the last 6000 years of Lake Grasmere's history. Several taxa were more common in these sediments than during later stages of the lake's development. These taxa include Macropelopia, Polypedilum, and Tanytarsus vespertinus.

Information on the ecological requirements of I. vespertinus is scarce. Schakau (1986) recorded this species as the dominant form in the fossil chironomid fauna from Lake Taylor, but in this study, no remains were found in surficial sediments from Taylor (Appendix, Table III.2.). This species has also been recorded from streams (Cowie, 1985; Boothroyd, 1987). In quantitative samples from the littoral zone of Lake Grasmere, Stark (1981) recorded I. vespertinus as the third most abundant chironomid (9.1% relative abundance) but occurring exclusively in one site group. This site group (D; Stark, 1981) comprised sampling sites at the southern end and western side of the lake in a water depth of 0-1 m. These sampling sites were characterized by a variety of substrate types with macrophytes most notable for their relatively stunted growth (possibly due to wave action and shallowness of the water) and very thick coatings of

periphyton and organic debris. I. vespertinus therefore appears to prefer shallow waters with vigorous water movements and plentiful organic matter available. Fossil remains of I. vespertinus having been more abundant during the oldest period of deposition of organic rich sediments in the core would support the suggestion of the existence of a shallower lake than at present, with a relatively high lake productivity.

The distributions of Macropelopia and Polypedilum are also of interest with regard to lower lake levels and higher lake productivity during this period.

Macropelopia (taxonomic designation as given in Chapter IV) is a taxon which may be mainly confined to the littoral zone of lakes. In recent collections by the author, larvae of Macropelopia were found mainly in samples from the littoral zone in Lake Grasmere, whereas Apsectrotanypus larvae were found mostly in mud samples collected from beyond the macrophyte beds in the profundal zone of Lake Grasmere. The author identified Macropelopia larvae as present in all samples collected by hand-net from the littoral zones of lakes and from wetlands in the Ashburton catchment in a biological survey (Stout & Burrows, in press.), but larvae of Apsectrotanypus were not found in these samples. Wilson (1989) collected Orthocladiinae and Tanypodinae larvae from weed fragments washed up into shallow waters along the western shore of Lake Grasmere. The Tanypodinae larvae were exclusively Macropelopia sp. The distribution of Macropelopia found in these studies suggests that Macropelopia may be a shallow water form. In the Lake Grasmere core, Macropelopia remains occurred with a relative abundance of as high as 1% to 6.3% (of the total fossils in the samples) only in the oldest organically rich sediments, when the lake may have been shallower than at present.

Polypedilum head capsules were found in most samples of the core below 55 cm but were most numerous in the oldest organically rich sediments and occurred in Groups VI and VII (derived from the cluster analysis, Fig. 5.3.) with 8.1% and 5.2% relative abundance (Table 5.2.). The maximum percentage occurrence of Polypedilum in these sediment sequences may be correlated to the suggested low lake level and the relatively higher lake productivity as indicated by comparative data

from several other studies. In the North Island, Boubee (1983) recorded Polypedilum spp. in highest numbers on the sandy edges of those Waikato lakes which had enriched but still moderately clear waters. In the seven Rotorua lakes studied by Forsyth (1978), P. pavidus larvae were found in low numbers in the two most productive lakes, Ngapouri and Okaro. In the South Island, Timms (1983) recorded Polypedilum in very low numbers from Lake Hawdon. Relatively low abundances of P. pavidus were recorded by Graham and Burns (1983) in the highly productive Lake Hayes down to a water depth of 10 m. High numbers of Polypedilum were found by Timms (1980a) in Lakes Rotoroa and Rotoiti, near Nelson. In these two lakes, Polypedilum occurred mainly in the shallower water at the inflow end, which had high inputs of allochthonous matter. Although Polypedilum is not a very common chironomid in lakes, this taxon appears to favour lakes with a relatively high productivity and in them occurs in the shallower regions.

In the oldest sediments of the core, a chironomid, Paucispinigera approximata, occurred that is uncommon at present in most South Island lakes. Head capsules of this taxon occurred only in the older sediments of the core and were not found above the 220 cm level. In the sediment sequence from 280 to 240 cm (Group V) P. approximata was the most abundant chironomid (Table 5.2.) and the 235 cm sample was classified by the cluster analysis as an outlier because 33% of all head capsules found in this sample belonged to this species.

The present-day distribution of P. approximata includes lakes which are surrounded by beech forests (Timms, 1982), as well as stream habitats in beech forests (Cowie, 1980, 1985; Winterbourn, 1982; Harding, in prep.). P. approximata occurred in Lakes Rotoroa and Rotoiti near Nelson, which have a considerable allochthonous input consisting of beech leaves and twigs (Timms, 1980a), and which might represent the substrate preferred by this chironomid. P. approximata is a collector-browser (Winterbourn, 1982) and feeds on fine particulate wood from amongst sediments and the surface of logs (Stark, 1981). Cowie (1980, 1985) found this species only in stream continua in beech forest catchments but not further downstream in catchments without beech cover. Winterbourn (1982) collected larvae of this species from a sample site in Middle Bush Stream which was within

a stand of mountain beech (Nothofagus solandrii var. cliffortioides). The results of the most recent study (Harding, in prep.) revealed that P. approximata was an important member of the chironomid community in four out of five beech forest streams in the Lewis Pass region. The high abundance of Paucispinigera in the older sediments might indicate a more complete beech forest cover of the catchment of Lake Grasmere than in present times. The disappearance of Paucispinigera before ca. 3400 years might point to a retreat of the beech forest from most of the lake shore, possibly due, for example, to reduction by natural fires.

In the late Holocene the frequency of natural fires increased in New Zealand. A study by Burrows and Russell (1990) indicated that fire was more prominent from 7000 yr B.P. in the central eastern South Island, with outbreaks occurring at irregular intervals up until recent times. The increase of fire frequencies, together with higher incidences of drought and erosion, was caused by the changing climate of the late Holocene towards colder temperatures with drier summers, similar to the present climate which was fully established by 3000 yr B.P. (McGlone et al., in press).

Some Nothofagus forest remains in the present catchment area of Lake Grasmere, on the ridge at the eastern side of the lake. Stark (1981) included in his studies sampling sites which received beech litter, but did not find larvae of P. approximata in these habitats. Therefore, it appears that this species might have disappeared from the lake before 3400 yr B.P. There has been no record of this species since except for one single head capsule found in the 23 cm sample, and pointing perhaps to an unsuccessful recolonization of the lake.

Corynocera, the dominant subfossil chironomid in Lake Grasmere, can be used as an indicator of a distinct substrate type. Larvae of Corynocera were found in lakes of the Waikato region which had clear waters with a maximum water depth of 1 m (Boubee, 1983). The sediments consisted of a flocculent organic layer with a high concentration of algae (mainly diatoms). Boubee (1983) considered Corynocera to be an indicator for low water levels and Deevey (1955) found exceptionally high numbers (up to 1500 head capsules per ml sediment) of this genus in fossil material from Pyramid Valley lake, which was shallow

throughout its history. But the consistency of the substrate appears to be a more important factor than the water level in influencing the distribution of Corynocera, possibly in association with very clear lake waters. Timms (1983) recorded Corynocera from Lake Letitia, near Cass, where larvae of this type were abundant down to a water depth of 12.5 m. Timms (1983) noted the special consistency of the mud which was "brown, very soft, and composed largely of small aggregates of flocculent material" (p.46). Corynocera was also the dominant chironomid in a surficial sediment sample from Lake Letitia (Fig. 8.4.). Lake Letitia was the only lake studied in the survey of chironomid remains from surficial sediment [illegible] sediment sample was 11.2 m, indicating extremely clear water.

In the sediments of the Lake Grasmere core, Corynocera occurred in high abundances when sedimentation processes remained stable. Throughout the core, except for the sediments above 50 cm in which Corynocera was not found, the distribution of this taxon was positively correlated with the water content of the sediments. Maxima in water content were correlated with maxima of Corynocera abundance, e.g. at the 300, 220, 150 and 100 cm horizon (Fig. 3.3. and Fig. 5.2.). Sediments which contained a larger amount of water are less compacted. Therefore the positive correlation of its distribution with the water content of the sediments indicates the preference of Corynocera for a more flocculent substrate type. The preference of this taxon for clear waters might be shown by the distribution of Corynocera in the oldest organically rich sediments of the core. At the 319 cm horizon, the end of the greater turbidity caused by the high input of clay and silt was indicated by increasing deposition of organic matter and increasing numbers of fossil remains. Although Corynocera was present in the 319 cm sample, this taxon did not become the dominant chironomid of the faunal assemblage until the 315 cm level. Possibly by this time lake waters had cleared adequately and the food availability in the form of benthic algae had increased sufficiently to favour higher growth rates in Corynocera than in the other Chironomidae in the community. Corynocera remained the dominant chironomid until the 285 cm horizon (sediment Groups VI and VII, Table 5.2.) above which Paucispinigera approximata became dominant (Group V,

Table 5.2.). In the sediments between 317 and 280 cm, Fragilaria blooms indicated abundant macrophytes in the lake. It appears that Corynocera is not associated with macrophytes; therefore, sufficient macrophyte-free sediment must have prevailed to allow the high abundance of Corynocera in these sediments. Larvae of this taxon have been observed to burrow into sediments and build branched tubes consisting of debris from the flocculant organic layer they live in (Boubee, 1983). The larvae can feed by protruding part of their body out of the tube and pulling lumps of algal/detrital material to the entrance of the tubes with the help of their mouth parts and prolegs. The organic material gathered is then eaten (Boubee, 1983).

Above the 280 cm horizon, visible changes in the sediment of the core could be correlated with low abundances or the absence of Corynocera. At the 260 cm level a 1 cm wide dark lamination was noted. In this sample, the relative abundance of Corynocera declined to a minimum in the older sediments of the core. A low organic matter and water content of the sediments in this sample indicated a possible short-term increase of mineral matter input. Between 250 and 220 cm, the water content of the sediments and the organic matter increased slightly. The abundance of Corynocera rose as well but remained generally lower than in the oldest organically rich sediments of the core. The nature of the sediment then changed considerably at 204 cm. The sediment layers in the following 8 cm contained a relatively large amount of sand particles. Such sand deposits can accumulate as the result of unusual storms which produce sufficient water currents and wave action to move sand out from the shore (Davis et al., 1985a). This is one possibility for a high country lake in the South Island. Another possible cause could have been a landslide due to an earthquake. Grant (1989) suggested that in New Zealand periods of increased frequencies of storms, erosion and alluviation, caused by changes of atmospheric circulation, alternated with tranquil intervals when erosion and sediment transport declined and soil formed. Head capsules of Corynocera were not found in the samples derived from the sandy layer of the core but this taxon occurred again in a relatively high abundance at the 195 cm level immediately after the deposition of sand had stopped.

Many of the other taxa of the chironomid community responded negatively to this disturbance and numbers of head capsules and taxa declined to a minimum in this sediment layer. Seven head capsules were found in the 204 cm sample, belonging to five taxa, and in the 200 cm sample only 4 head capsules occurred, which belonged to four taxa. The number of head capsules in these samples is too small to provide statistically meaningful results but the taxa appear to belong to mostly littoral forms. These were especially Cricotopus sp. 25, Paratanytarsus, which occur in shallow standing waters (Stark, 1989), and Polypedilum in the 204 cm sample, and Chironomus, which can occur in the profundal or littoral areas of a lake, and Paratanytarsus in the 200 cm sample. The littoral element in these samples might indicate that these head capsules were transported into the lake with the mineral input, which included sand from the littoral areas.

In the sediment layers above 195 cm, the contents of water and organic matter of the sediments increased continously up to the 170 cm horizon above which both sediment parameters remained relatively high and stable until the 60 cm level in the core (Fig. 3.3.). The faunal composition of the sediments between the dominant chironomid between 195 and 160 cm, its relative abundance was generally lower than in the succeeding sediment layers, and Chironomus and Apsectrotanypus were also relatively abundant (Fig. 5.2.). This composition of the fossil fauna might have been caused by slightly more compacted sediments in the layer between 195 and 160 cm, in which the water content was lower than 50% of wet weight and the organic matter content was lower than 8% of dry weight. cm, in which tcm horizon, the water content in the sediments remained between 52% and 65% and the organic matter content was on average 2.5% higher than in the older sediments (with the exception of the oldest organically rich sediments between 313 and 295 cm) indicating a more flocculent substrate. Corynocera occurred in high numbers (Appendix, Table II.3.) and very high abundances above the 160 cm horizon (40% relative abundance, see Table 5.3., sediment groupings II and III) indicating a stable environment for about the next 1500 - 1700 years. The sediments during these times must have contained a high percentage of benthic algae and the lake waters would have been highly transparent as is suggested by the high percentage

occurrences of Corynocera which favours these conditions. The abundances of Chironomus and Apsectrotanypus are generally lower in these sediment layers and the composition of the entire fauna remained relatively constant until the 60 cm horizon.

In the most recently deposited sediments of the core (55 cm - top), a major shift in faunal composition occurred. This sediment layer is represented in the cluster analysis by Group I (Fig. 5.3. and Table 5.2.). Corynocera disappeared entirely, suggesting a sedimentation-related disturbance. At 55 cm in the core, numbers of chironomid remains as well as taxa declined suddenly although no apparent change in the sediments of the core was discernible. A colour change and an increase of organic matter in the core occurred between 30 and 22 cm (Fig. 3.2.). The succeeding sediments were a sequence of alternating pale and light olive grey implying a rapid change in sedimentation pattern during the last 1000 years. At this stage of the study, it is not possible to determine the exact mechanism which governed the sudden change in the faunal composition at the 55 cm horizon. A possible explanation could be a change in the lake area caused by encroachment of the New Ribbonwood Fan. As mentioned earlier, deposition in the fan still continued in historic times (Gage, 1959).

The development which began at the 55 cm level culminated at the 40 cm level. The water content and the organic matter content of the sediments declined to a minimum in this sediment horizon (35.2% and 5.7 % respectively). Numbers of head capsules and chironomid taxa also declined to a minimum of two head capsules and one fossil taxon (Orthocladiinae sp. IX). These results show that the changes in the environment must have been considerable. The diatom flora (Fig. 3.4.) also changed above the 60 cm horizon. Epiphytic diatoms, especially Fragilaria (Fig. 3.5.), decreased, whereas facultative planktic diatoms, especially Cyclotella stelligera, increased in relative abundance indicating two possibilities: an increase of the water level and/or an increase in turbidity. The encroachment of the New Ribbonwood Fan on the lake could have caused the rise of the lake level through damming of the lake, and could have caused higher turbidity of the lake waters through resuspension of the finer inorganic material originally deposited in the littoral zone of the lake. A change in the substrate type available to Corynocera could

have resulted from the sedimentation of a larger amount of inorganic material which would have compacted the sediments. Increased turbidity would have caused the inhibition of the growth of benthic algae. Both changes would have destroyed the basis of survival for Corynocera. Above the 55 cm level, only one head capsule of Corynocera was found (in the 27 cm sample).

The disappearance of a fossil taxon from a core does not necessarily prove that the taxon did not live in the lake anymore. The area of distribution of the living larvae could have changed to such an extent that the fossil remains would not be deposited at the site of the coring. That appears unlikely in the case of Lake Grasmere because the lake is small and remains of littoral taxa were found in varying amounts in all samples from the core. Corynocera was not recorded either by Stark (1981) or Timms (1982, 1983), nor were its remains found in the surficial sediment sample collected from Lake Grasmere in this study (see Chapter VIII). Therefore it is reasonable to suggest that Corynocera disappeared from Lake Grasmere about 1200 years ago.

It is interesting to note the changes in the composition of the fossil chironomid fauna in the 55, 50 and 40 cm samples. In the 55 cm sample, Paratanytarsus fossils were found with a relative abundance of 30% which is the maximum abundance of this taxon in the core. A high relative abundance of Paratanytarsus was recorded in the 30 cm sample (22%) and in the samples derived from the sediment layer containing Grana minora particles (204 cm - 14.3%, 200 cm - 25.0%). Paratanytarsus inhabits shallow standing waters (Langton et al., 1988; Stark, 1989) living on substrates close to the water's edge and amongst emergent vegetation. Boubee (1983) found this species as the dominant or sub-dominant chironomid at the edges of the lakes, or amongst submerged macrophytes or reeds, in several Waikato lakes. Paratanytarsus was dominant in the centre in only two shallow lakes (L. Waahi, 5 m, L. Rotorua, 6 m). Fossil head capsules found in the core would have been derived through off-shore displacement caused either by resuspension of sediment or an off-shore transport of littoral material. This possibly happened in the sediment layer containing the sand particles (204-200 cm). The high relative abundance of Paratanytarsus in the 55 cm sample was not caused by an increase in the number of Paratanytarsus head capsules but by a marked

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decrease in the numbers of other chironomids, mainly Chironomus and Corynocera (Appendix, Table II.3.). This result could indicate that the change in the environment had a greater influence on the profundal than on the littoral fauna. This trend was continued in the 50 cm sample in which the dominant species, besides Chironomus, was Eukiefferiella claripennis (28.6% relative abundance). In this study, E. claripennis was mainly found in streams in the Cass area and on the West Coast (author's identification of larvae in the collections by R. Death and P. Ryan, respectively). The sub-dominant species in the 50 cm sample was Tanytarsus vespertinus, an inhabitant of the littoral zone of lakes. In the 40 cm sample only one head capsule of Orthocladiinae sp. IX was found. It is difficult to imagine what caused the almost total obliteration of the chironomid fauna in this sample. Perhaps there was a high short-term input of mainly alluvial or terrestrial material, although the sediments of this sample did not contain sand particles.

Another factor which added to the instability of the environmental conditions in the lake during the last 1000 years was the appearance of the first Polynesians; in particular their influence on the landscape of the Cass Basin through use of fire (McGlone, 1989; McSaveney & Whitehouse, 1989). The increase of grass pollen at the 30 cm level in the core correlated with an initial increase in organic matter followed by the maximum in organic matter in the core and the pronounced peak in the abundance of Orthocladiinae sp. IX between 27 and 20 cm (Fig. 5.2.). The large amount of organic matter in these sediment layers might indicate a rise in lake productivity and increased nutrient input caused by the frequent fires in the early period of Polynesian settlement (Bradbury, 1986b). The nutrient input appears to have supported mainly the growth of macrophytes. Macrophytes must have been more abundant than today during this period of high organic matter deposition, as was indicated by the high abundance of Orthocladiinae sp. IX.

In collections by the author in the South Island, undescribed larvae of this genus have been found exclusively in lacustrine habitats in which these larvae live closely associated with macrophytes. Larvae of this taxon were collected from shallow ponds in the Botanic Gardens, Christchurch, where they occur in large numbers amongst the water-lily

species during the winter months. The larvae were observed to move over the leaves and sometimes burrow into the leaves and remain there until pupation. When burrowing into the leaves, the larvae leave cleared tunnels behind them. Apparently, larvae of Orthocladiinae sp. IX can feed by shredding living macrophytes. The vascular plant herbivory of Orthocladiinae sp. IX would be consistent with its mainly lacustrine distribution, as most shredder-herbivores are lentic and relatively rare in streams (Newman, 1991). In Lake Grasmere, larvae of Orthocladiinae sp. IX were collected from sites with macrophyte growth but were not found in mud samples from the deeper areas of the lake. High relative abundances of Orthocladiinae sp. IX were found in surficial sediment samples derived from lakes with extensive macrophyte beds, e.g. the chironomid assemblage in the Lake Marymere sample was dominated by Orthocladiinae sp. IX (81% relative abundance), as well as those in the samples from Lake Georgina (46%) and Lake Evelyn (51%) (see Chapter VIII). This taxon is therefore considered to be an indicator species for the presence of macrophytes.

The distribution of Orthocladiinae sp. IX throughout the core showed only the one marked maximum of abundance in the younger sediments (cluster Group I). In most samples of the core remains of this taxon were present only in relatively low abundances (Fig. 5.2.) and Orthocladiinae sp. IX was absent in sediment layers with high mineral input (204-200 cm, 260 cm, and 326-320 cm). A slight maximum of abundance of Orthocladiinae sp. IX was found in the first two samples after the cessation of the clay and silt deposition (319 and 318 cm) indicating the presence of macrophytes. Above the 318 cm horizon the dominance pattern of the fossil chironomid fauna changed and the relative abundance of Orthocladiinae sp. IX decreased and that of Corynocera increased in the above sediment layers. Whereas Orthocladiinae sp. IX is closely associated with macrophytes, Corynocera favours flocculent sediment with a high concentration of benthic algae. High percentages of epiphytic and epilithic diatoms in the oldest organically rich sediments of the core (Fig. 3.4.) indicated abundant macrophytes in a shallow lake. Thus, although there must have been enough macrophyte-free sediment available above the 318 cm horizon to allow the growth of the dominant Corynocera, there would have been considerable macrophyte beds still in the lake to support larvae of Orthocladiinae sp. IX. But abundances of Orthocladiinae sp.

IX remained relatively low above the 318 cm horizon so that some other as yet undetermined factor besides the presence of macrophytes governed the distribution of this taxon throughout the core.

Orthocladiinae sp. IX appears to be cold-adapted and later instar larvae are found in greater numbers during the winter months. During rearing experiments from larval stages with this taxon, it was found that higher survival rates were obtained by placing larvae in 4°C temperature controlled rooms whereas the larvae kept in 10°C or 15°C mostly died (pers. obs.). Stark (1981) found only low numbers of Orthocladiinae sp. IX larvae (named Orthocladiinae sp. A in Stark's thesis) during his quantitative sampling program, and only at sampling sites at the southern end of the lake at a water depth of 1 m. The number of larvae found was higher in winter months. Wilson (1989) collected chironomid larvae from weed fragments washed up onto the substrate in shallow waters along the western shore of Lake Grasmere during late winter in 1989. She found only Macropelopia larvae and two species of orthoclads, Cricotopus sp. and Orthocladiinae sp. IX. The authors's own collections in the ponds of the Botanic Gardens revealed high numbers of larvae in June and July but not in late spring and summer. Fourth instar larvae were also numerous in a sample collected from the Chara sp. beds in shallow waters from Lake Georgina in early winter (on 31 May, 1990).

Besides being cold-adapted, Orthocladiinae sp. IX larvae are not dependent on only one macrophyte species. As shown above, larvae of this taxon have been found on leaves of Nymphaeaceae species, amongst Chara spp., and Lemnaceae species (pers. obs.), on Elodea canadensis and Isoetes alpinus fragments (Wilson, 1989), and amongst I. alpinus and Myriophyllum propinquum. Therefore, it appears that as a cold-adapted species and dependent on macrophytes, adult emergence occurs for this species during the colder winter months (in a country with a temperate climate) as long as there are macrophytes available which do not die back in winter.

In order to answer the question why Orthocladiinae sp. IX was not more abundant during most of the past 6000 years of Lake Grasmere's history, it may be suggested that the change to a more flocculent sediment prevented macrophytes from spreading over most of the lake

floor during the period the lake was shallow. Macrophytes at the periphery of the lake might have had a significant population of Orthocladiinae sp. IX, whose fossil remains might have been partly trapped in the macrophyte beds instead of being transported to the area of the lake where the coring site was located. But this remains speculation and the biology and ecological requirements of Orthocladiinae sp. IX will need more research.

Besides Orthocladiinae sp. IX, the taxon Cricotopus is also closely associated with macrophytes. Many Cricotopus species live epiphytically on submerged macrophytes, grazing on diatoms and algae, with some species being adapted to mine macrophytes (Hirvenoja, 1973). Observations on the gut contents of Cricotopus spp., collected in the South Island (Stark, 1981), showed that the main dietary components in the larvae studied were algae and detritus. Therefore Cricotopus appears to be a herbivorous collector-browser whereas Orthocladiinae sp. IX is most probably a macrophyte-shredder. In samples collected from the macrophyte zone in Lake Grasmere (Stark, 1981), larvae of Cricotopus were clearly the dominant chironomids, making up 70.4% of the total material collected. The sub-dominant chironomids were Macropelopia and Gressittius (13.5%). The importance of Cricotopus in Lake Grasmere was also corroborated by observations of the faunal composition found in the surficial sediment sample, in which Cricotopus head capsules were the third most abundant remains after Apsectrotanypus, which was sub-dominant, and the dominant Chironomus (see Chapter VIII). Both, Chironomus and Apsectrotanypus are present day inhabitants of the profundal zone in Lake Grasmere. But fossil remains of Cricotopus in profundal sediments are derived from the littoral zone through off-shore transport, as Cricotopus larvae are inhabitants of the macrophyte zone. The occurrence of a relatively high abundance of Cricotopus remains in a profundal sediment sample might be a reflection of the existence of a relatively large population of Cricotopus in the littoral zone of Lake Grasmere.

The oldest sample in the core, in which Cricotopus head capsules appeared was the 317 cm sample (Fig. 5.2.). In that sample the shift in dominance from Orthocladiinae sp. IX to Corynocera had occurred. In the sediments above the 317 cm horizon Cricotopus was present in most samples (Fig. 5.2.) and frequently occurred with a slightly higher

abundance than Orthocladiinae sp. IX. Cricotopus did not occur in the samples between 204-200 cm and 50-30 cm, the sediment layers which represented environmental disturbances. In the layer 27 to 20 cm, the period of dominance of Orthocladiinae sp. IX, Cricotopus occurred only in low relative abundances and was found above that sediment layer only in the 14 cm sample (25% relative abundance), in the 10 cm sample (6.3%) and the top sample of the core (19.2%). At the top of the core Cricotopus was the sub-dominant taxon.

As shown earlier, macrophytes must have been present throughout the last 6000 years in Lake Grasmere, but it appears that Cricotopus became abundant only during very recent times. This taxon was not very successful during the period of increased organic matter deposition (27-20 cm) when the dominance of Orthocladiinae sp. IX indicated an increase of the macrophyte cover in the lake. A possible explanation for the increase in abundance of Cricotopus being only recent might be the change in the composition of the macrophyte flora in Lake Grasmere during the European settlement period.

Elodea canadensis, a native of North America, has been in New Zealand for over 100 years (Hughes, 1976). The timing of introduction to Lake Grasmere is not known, but E. canadensis was present in Lake Sarah in 1934-1935 (Flint, 1938). In the present day lake, this macrophyte forms dense beds in mesotrophic Lake Grasmere and excludes other macrophyte species at depths ranging from about 0.5-1.2 m to 7 m (Stark, 1981). The original macrophyte flora of Lake Grasmere, before the introduction of Elodea, may have been composed of charophytes and Potamogeton in the deeper waters of the lake and of mixed native species of Myriophyllum, Potamogeton and Isoetes in shallower water (see Stout, 1975b and references therein). Cricotopus apparently invaded the Elodea zone of Lake Grasmere more successfully than Orthocladiinae sp. IX. Cricotopus larvae were found at all sampling stations in the macrophyte zone of Lake Grasmere by Stark (1981). Cricotopus favoured site groups C and D and made up 87.9% and 64.5%, respectively, of the total chironomid fauna found in samples from these site groups (Table 3.14 in Stark, 1981). The flora of site C was exclusively E. canadensis and site group D contained one sample with E. canadensis. The remaining samples of site group D contained Isoetes alpinus (WI and SI) and Myriophyllum propinquum (SM) (Stark, 1981,

Table 3.3.). Larvae of Cricotopus seem to inhabit the entire macrophyte region of Lake Grasmere without showing a preference for any macrophyte species. This would be consistent with the feeding mode of these larvae which are herbivorous browsers.

Although Orthocladiinae sp. IX was observed amongst several species of macrophytes and Wilson (1989) apparently found larvae of this taxon in fragments composed of Elodea and Myriophyllum, Stark (1981) recorded Orthocladiinae sp. IX in low densities only from his sites SI and SM, which contained Isoetes and Myriophyllum respectively. More research on the biology of Orthocladiinae sp. IX is needed, and whether this taxon can utilize Elodea as a food or not should be tested in future research.

As described above, Orthocladiinae sp. IX showed a maximum in relative abundance between 40 and 20 cm in the core, and remained one of the dominant chironomids until the 12 cm layer. But whereas this taxon accounted for over 50% of the fossil chironomid fauna in the samples between 27 and 23 cm, from the 17 cm sample upwards in the core the abundance of Orthocladiinae sp. IX began to decline and the community structure of the fossil chironomid fauna changed. In the 17 cm sample, Chironomus occurred with the same abundance as Orthocladiinae sp. IX; in the 14 cm sample, three species occurred each with 25% relative abundance: Chironomus, Corynocera, and Cricotopus; and in the 12 cm sample, four species occurred with 20% relative abundance: Chironomus, Chironomini sp. A, Corynocera, and nr. Pentaneura (Fig. 5.2.). This change in community structure between 17 and 12 cm was accompanied by a decline of organic matter content in the sediments from 17.2% in the 25 cm sample to 6.4% in the 14 cm sample (Fig. 3.3.) and a decline in the water content to 42.8% of wet weight in the same sample (Appendix, Table II.1.). The core stratigraphy of this sediment zone (Fig. 3.2.) showed thin differently coloured sediment layers indicating a rapid change in the sedimentation regime at that time. The low concentrations of water and organic matter in this sediment layer pointed to a phase of increased mineral input into the lake. As could be observed during earlier phases of increased input of minerogenous matter, this was reflected in a decline in the density and diversity of the fossil chironomid fauna. The number of chironomid taxa decreased from 12 taxa in the 23 cm sample to four taxa in all samples

between 17 and 6 cm; the number of remains declined from 145 in the 23 cm sample to five head capsules in the 12 cm sample (Fig. 5.1.; Appendix, Table II.2.). This fossil density is only slightly higher than that in the 40 cm sample and comparable to that in the sediment layer containing the Grana minora particles (204-200 cm). The increased sediment input into the lake was probably caused by increased erosion due to a reduction of the vegetation cover of the lake's catchment through burning by Polynesian people (McSaveney & Whitehouse, 1989).

Towards the top of the core, the abundance of Orthocladiinae sp. IX decreased down to 3.8% relative abundance in the top sample. Chironomus became the dominant chironomid above the 10 cm horizon (Fig. 5.2.). At this level the number of remains and taxa began to increase again. The 6 cm at the top of the core covered the time of European settlement in the area and the dominance of Chironomus might indicate a slight shift to mesotrophy (Graham, 1976; Forsyth, 1986; Schakau, 1986). High larval densities of Chironomus zealandicus were recorded by Robb (1966) in oxidation ponds of the Christchurch Drainage Board's Sewage Treatment plant. Annual mean production of C. zealandicus in eutrophic Lake Ngapouri (Forsyth, 1986) was comparable to that of C. plumosus in eutrophic Federsee in South-West Germany (Frank, 1982). C. plumosus is used as an indicator species for eutrophic lake waters in Europe (Sæther, 1975). The annual mean production of C. zealandicus in eutrophic Lake Hayes, South Island, was three times higher than in both Lakes Ngapouri and Federsee, and Graham and Burns (1983) showed a direct relationship between phytoplankton productivity and chironomid production (primarily that of Chironomus zealandicus). The large numbers of Chironomus zealandicus in eutrophic lakes in New Zealand supports the interpretation that high abundances of fossil Chironomus in cores indicate a possible increase in trophic state.

During this period represented in the core by the layer 10-1 cm, Apsectrotanypus became the sub-dominant chironomid of the fossil chironomid fauna. An exception was found only in the top sample, in which Cricotopus was sub-dominant. Boubee (1983) regarded high abundances of Chironomus together with Tanypodinae as an indication of open water and a reduced littoral area. In the surficial sediment

sample from Lake Grasmere (see Chapter VIII), Chironomus was the dominant taxon occurring with 32% relative abundance, Apsectrotanypus was the sub-dominant form with 24% relative abundance, followed by Cricotopus with 15% relative abundance. Throughout the core, Apsectrotanypus occurred in some samples in high relative abundances but mostly not coinciding with high abundances of Chironomus in the same samples. This is especially obvious in the older sediments of the core (240-280 cm, Fig. 5.2.) in which Apsectrotanypus had a maximum in abundance whereas the abundance of Chironomus remained relatively low in the samples derived from this sediment layer. Therefore, the high relative abundances of both Apsectrotanypus and Chironomus in the youngest sediments might support the conclusions derived from the fossil diatom analysis that the lake level of Lake Grasmere rose to its present depth only during relatively recent times.

Precise information about the present day distribution of Apsectrotanypus is not available because in most studies there has been no distinction between different genera of Macropelopiini. But Timms (1983), in his study of the benthos from seven Cass lakes, included only Gressittius antarcticus and Macropelopia umbrosa (in this study designated as Apsectrotanypus) in the taxon he listed as Macropelopia spp. Head capsules of Gressittius were rare in all surficial sediment samples from South Island lakes (see Chapter VIII), so that it is probable that most larvae in Timms' study would have been Apsectrotanypus. In Timms' study, Macropelopia spp. were dominant in Lakes Letitia and Pearson, and sub-dominant in Lakes Grasmere, Marymere, and Lyndon. Furthermore, Macropelopia spp. were dominant in the brown water Lakes Gault and Matheson (Timms, 1982) and common or abundant in the benthos of almost all twenty South Island lakes in the study (Timms, 1982). In his study larvae of this taxon were absent only from shallow athalassic Salt Lake, Sutton. Macropelopia spp. (excluding G. antarcticus) occurred as the third most common chironomid in eutrophic Lake Hayes (Graham & Burns, 1983). Macropelopiini, and very possibly mostly Apsectrotanypus, appear to have a broad niche and can survive in a wide variety of ecological conditions, except perhaps in waters with high salinity and low temperatures. In short cores from Lake Monowai, one of the deep, cold, and oligotrophic lakes in the south of the South Island, Tanypodinae head capsules accounted for only 2.2% of the total fossils (Schakau,

1986). The ability to survive in a wide variety of conditions might be partly due to the mode of feeding of these larvae. Tanypodinae are facultative predators and Stark (1981) found in the gut contents of Macropelopia spp. larvae, collected from sites throughout the South Island, that the main dietary components were diatoms and detritus. Less common were prey items such as other chironomid larvae and Cladocera (mainly Graptoleberis testudinaria and Bosmina meridionalis).

In the core from Lake Grasmere Apsectrotanypus head capsules were the third most abundant chironomid fossils and accounted for 9.3% of the total fossils. This taxon was common in most samples and this is perhaps a reflection of its broad niche. Apsectrotanypus appeared first in the 319 cm sample and became abundant in the sediment Group V (Fig. 5.2., Fig. 5.3., Table 5.2.), which covered the period when P. approximata was the dominant chironomid. Both taxa had a high relative abundance in the 260 cm sample (Fig. 5.2.). This sample was characterized by small amounts of sedimentary water and organic matter, indicating increased mineral input, and many chironomid taxa reacted negatively to it. It is possible that P. approximata was less influenced by the increase in minerogenous matter input because this taxon was dependent on allochthonous input (e.g. beech litter) whereas Apsectrotanypus was less influenced through being a predator. In Lake Temiskaming (Sallenave & Barton, 1990), only the distribution of the tanypod Procladius, a facultative predator, was positively correlated with turbidity.

Further up in the core, Apsectrotanypus occurred in relatively high abundances until the 60 cm horizon. In the sediment layers above 55 cm, when Orthocladiinae sp. IX reached its maximum abundance, head capsules of Apsectrotanypus were absent in most samples from this period (55-12 cm). As mentioned before, the change in the environmental conditions between 55-40 cm must have been marked, and most chironomid taxa were not found in this sediment layer. But between 30 and 20 cm a period of relatively high lake productivity was indicated, and the number of chironomid taxa increased from one taxon in the 40 cm sample to 12 taxa in the 23 cm sample. It is not possible at present to determine the exact factors which inhibited the growth of Apsectrotanypus between 55 and 12 cm but considering the broad

niche of this taxon it would be important to clarify this question by future research.

A further chironomid taxon, which disappeared entirely in the younger sediments of the core but reappeared in the two most recent samples with an increasing relative abundance, was Cladopelma curtivalva. Below the 50 cm horizon, Cladopelma was present in most samples with the exception of samples collected from periods with increased turbidity (204-190 cm, 260 cm, and 326-320 cm). Boubee (1983) recorded Cladopelma from lakes in the Waikato among beds of Characeae. Distribution data from the North Island presented by Boubee (1983), Forsyth (1976, 1978), and Forsyth and McCallum (1981) suggested that Cladopelma is a species whose maximum depth distribution is linked to light penetration and perhaps indirectly to the presence of characean meadows. The preference for clear waters might explain the negative response of Cladopelma to incidences of high turbidity during the last 6000 years of Lake Grasmere's history. In South Island lakes, the distribution of Cladopelma does not appear to be linked to that of Characeae. Stark (1981) did not record Cladopelma larvae from the littoral zone of Lake Grasmere, but Timms (1983) recorded Cladopelma in benthic mud samples in nearly all Cass lakes studied. In Lake Grasmere, larvae of this taxon occurred with 14.4% relative abundance (percent of all larvae collected). In Lake Letitia, Cladopelma occurred down to a depth of 12.5 m and a multiple regression analysis revealed that the distribution of Cladopelma was mainly controlled by a depth-related factor and by the organic matter content of the sediments (Timms, 1983). Timms (1983) explained the depth limitation of Cladopelma by a low tolerance to partial deoxygenation, which can occur in Lake Letitia. The same reasoning was used by Graham and Burns (1983) to explain the distribution of Cladopelma in eutrophic Lake Hayes where it occurred only down to 10 m depth. Thus, if Cladopelma preferred relatively high concentrations of organic matter in the sediments and did not occur amongst macrophytes, the low organic matter content in most samples of the Lake Grasmere core would have limited the numbers of Cladopelma during most periods of the last 6000 years of the lake's development (Fig. 5.2.). Increased macrophyte cover during the earlier phase of higher organic matter deposition (27-20 cm) might have favoured Orthocladiinae sp. IX. Corynocera had perhaps a competitive advantage in the more flocculent sediments of

the older phase of increased organic matter deposition (313-295 cm). In Lake Letitia, Corynocera and Cladopelma had the same depth distribution, but Cladopelma occurred with only 6.2% relative abundance, whereas Corynocera occurred with 16.5% relative abundance (Timms, 1983).

In the detrended correspondence analysis on the samples from the core based on the relative abundances of the fossil chironomid taxa (Fig. 5.5.), the ordination axes are hypopthetical environmental variables (ter Braak, 1988) on which the samples are ordered according to an environmental gradient. For example, Kansanen et al. (1990) used DCA to order Chironomidae and Oligochaeta species from different sampling stations in a Finnish lake along a water pollution gradient.

The environmental gradient, which resulted from the detrended correspondence analysis on the Lake Grasmere samples, may be explained as a gradient of substrate types. Different substrate types were prevalent during certain periods of the last 6000 years of Lake Grasmere's history. Substrate is an important factor for determining the species composition of the chironomid fauna (Rossaro, 1991a) as well as regulating the density of chironomids (Brennan et al., 1978). Maitland (1979) investigated the distribution of zoobenthos and sediments in Loch Leven, Scotland, showing that two distinct communities could be determined on two different substrate types, e.g. sand or mud. Moss and Timms (1989) identified sediment stability as one of the major determinants of benthic populations in a series of shallow lakes in England. Studying the benthos of seven lakes in the Cass region, including Lake Grasmere, Timms (1983) noted the differences in sediment texture between the lakes and suggested that the sediment texture was partly responsible for the differences in the composition of the benthic communities in these lakes.

The samples of the Lake Grasmere core were ordered along the ordination axis based on the relative abundances of four main species: Corynocera, Chironomus, Orthocladiinae sp. IX, and Paucispinigera approximata. Larvae of Corynocera prefer flocculent, soft mud containing a high density of benthic algae; larvae of Chironomus show a preference for fine mud with a varying degree of mineral or organic matter, although Boubee (1983) found Chironomus zealandicus larvae

usually in organically rich mud in lakes in the Waikato region. Orthocladiinae sp. IX larvae are associated with macrophytes. This gradient is given on axis one. The gradient does not follow exactly the time series of the samples as Orthocladiinae sp. IX, which has the highest scores on axis one, was important in the sediments between 30 and 20 cm, and Chironomus, which was dominant in the youngest sediments, had scores between those of Corynocera and Orthocladiinae sp. IX. High scores on axis two (Fig. 5.5.) demonstrate the importance of allochthonous input, as Paucispinigera approximata was abundant in all samples with high scores on the second axis.

In summary, the limnological conditions in Lake Grasmere changed considerably during the last 6000 years. Long periods with a relatively stable environment, reflected by high relative abundances of certain chironomid taxa and a comparatively unchanging faunal composition, were disrupted by short-term but high magnitude disturbances resulting in a decline of chironomid diversity and abundances. Shifts in community structure were mainly due to changes in substrate type. Substrate type changes were caused by variations over time of such factors as mineral input, macrophyte cover, lake productivity and possibly changing lake level. The fossil chironomids from Lake Grasmere have been good indicators of the general changes which have occurred in this geologically active environment of the Southern Alps of New Zealand.

CHAPTER VI

FOSSIL CLADOCERA

6.1. Introduction

Cladocera are small Crustacea which mainly occur in freshwater environments. They form an important component of the communities of the plankton and littoral habitats of freshwater lakes. There are approximately 420 species in eleven families.

The exoskeleton of many species is preserved in the sediments and can be identified in many cases to species level (Frey, 1987). Two major groups of Cladocera leave remains in lake sediments: the planktic Daphniidae and Bosminidae and the benthic Chydoridae, and very rarely Macrothricidae (Whiteside & Swindoll, 1988, Brugham, 1983).

The Chydoridae inhabitat chiefly the littoral zone of lakes. The major microhabitats utilized by species of Chydoridae within the littoral zone are the bottom sediments, bottom structures (e.g. rocks or logs), submerged plants, and the open water column (DiFonza & Campbell, 1988). The distribution of certain chydorid species appears to be closely related to the presence or absence of vegetation and the nature of the substrate (Duigan & Kovach, 1991). Some species have also been grouped according to their preference for clear waters or tolerance of polluted waters (Hofmann, 1978, 1986b). Although most Chydoridae live in the littoral, their remains are transferred offshore by currents and become completely integrated by relative abundance of species, e.g. according to their proportion in the living community, before incorporation into the sediment. Therefore, the percentage distribution of species in the sediments provides a good record of the chydorid community in the entire lake, integrated over habitats and time (Hofmann, 1987; Frey, 1988).

Amongst the planktic Cladocera, common open-water species belong to Daphnia, Bosmina, and Ceriodaphnia. These Cladocera are less common in vegetated areas, and it has been shown that rooted aquatic plants have a repellent effect on some planktic species, especially Daphnia

(Pennak, 1973). The species composition of limnetic Cladocera appears to be partly regulated by predation from other invertebrates and from fishes. Planktivorous fishes select large, visible zooplankton and can therefore cause a replacement of large zooplanktic forms by small-bodied forms (Kerfoot, 1974). Invertebrates select small individuals as prey, which can cause alterations in prey morphology. Bosmina offers a good example of changes in prey morphology in response to invertebrate predation. Bosmina with long spines and antennules are more adept at escaping copepod predators but are less common in the absence of copepod predators (Whiteside & Swindoll, 1988).

Besides biotic factors, such as predation, algae or macrophytes, Cladocera communities are influenced by a variety of abiotic factors, including water chemistry, transparency of the water, lake morphology and water depth, and lake productivity. Cladocera communities respond to a lowering of transparency. Large amounts of inorganic materials reduce species diversity and abundance. Water level changes over the course of a lake's ontogeny may alter substantially its morphometry and consequently the relative abundance of littoral or limnetic organisms. Lakes with a limited littoral zone (and more open water and a greater water depth) have a low abundance and diversity of inshore species - namely the Chydoridae - and the fossil assemblages are predominantly limnetic Bosmina and Daphnia. The planktic/littoral ratio (Bosmina versus Chydoridae) is used to indicate palaeo-water levels (Alhonen, 1970; Whiteside & Swindoll, 1988). An increase in lake productivity can have several effects, e.g. in some lakes in the northern hemisphere a succession of Bosmina species occurred with increasing eutrophication (Hofmann 1978, 1986b; Boucherle & Züllig, 1983). The response of the littoral chydorids to changes associated with increasing lake productivity (the replacement of "clear-water" species by "polluted-water" species, Hofmann, 1986b) appears to be slower than that of the limnetic forms. The chydorid population does not begin to change until eutrophication affects the littoral habitat itself, for example when macrophytes are eliminated by algal blooms (Frey, 1988).

6.1.1. Cladocera in Palaeolimnological Research

As the structure and composition of Cladocera communities respond to changing environmental conditions, and as they leave remains in sufficient numbers in lake sediments, their fossil assemblages can be used as biological indicators of changing conditions during the history of the lake and its catchment. Several authors have described the importance and applications of analyses of cladoceran microfossils from lake sediments in Quaternary palaeoecology (Frey, 1960, 1964, 1976, 1986; Hofmann, 1987; Whiteside & Swindoll, 1988). Fossil Cladocera have been used frequently to document post-glacial environmental change (Frey, 1958; Goulden, 1966; Harmsworth, 1968; Hofmann, 1978, 1983a, 1986b, 1991; Goulden & Vostreys, 1985; Hann & Warner, 1987), the impact of prehistoric settlements (Szeroczyńska, 1991), and human disturbance (Brugham & Speziale, 1983) and in more applied aspects of recent environmental impact investigations, e.g. anthropogenic eutrophication and acidification (Uimonen-Simola & Tolonen, 1987).

The present study constitutes the second investigation of fossil Cladocera from lake sediments in Australasia. The first study was Deevey's (1955) analysis of the microfossils of the Upper Swamp deposit in Pyramid Valley, which included fossil Cladocera remains. The objectives of the present study are to gain information about the long-term development of Cladocera populations in lakes, about the responses of Cladocera to changes in limnological conditions, and to investigate whether or not it is possible to infer limnological changes from the succession of fossil cladoceran assemblages. The stratigraphy of the fossil Cladocera from Lake Grasmere will be compared with those of the fossil Chironomidae, diatoms, and fossil pigments.

6.2. Methods

The preparation of quantitative slides for the Cladocera counts has been described in Chapter II. The estimate of remains per ml of sediment was based on an aliquot fraction on 10 "Cladocera slides" per sample, or if the fossil densities were too low, on the total number of Cladocera remains counted from all slides prepared from one sample.

The slides contained exoskeletal components either intact or as fragments. Fragmentation of Cladocera remains could have been caused by predation on living animals, or by activities of invertebrates in sediments processing detritus and remains; also by physical destruction in high-energy environments, or during the preparation of the slides. To take the fragmentation into account for the construction of the percentage composition of fossil cladoceran assemblages, each fossil encountered for a given species was tabulated under the appropiate exoskeletal category and the degree of fragmentation was noted. The calculation of whole animals from the fragmented remains was undertaken according to the formulae given by Frey (1986, Table 32.1, p. 678-679). The abundance of each of the different exoskeletal components was calculated for each species present. The exoskeletal part with the highest abundance was then taken as the most likely estimate of the abundance of the species in the particular sample (Frey, 1986). The raw data of the cladoceran microfossil counts are presented in Appendix II, Table II.4.

A reference collection of whole animals of most Chydoridae species was prepared to help with the identification of the microfossils. These Chydoridae were collected from a variety of sites in the South Island by the author, and are kept in the Zoology Department of the University of Canterbury. The collection also includes slides of Australian Chydoridae provided by Dr. R. Shiel. Chydoridae were fossilized (dissolving the tissue of the animals leaving only the exoskeletal parts) by heating the chydorids in concentrated hydrochloric acid (Frey, 1986). This method provided material to show the fine morphological details used to identify the microfossils.

6.3. The Distribution of Cladocera in New Zealand

The Cladocera fauna of New Zealand consists of 40 described species (Forsyth & Lewis, 1987). Many New Zealand species occur also in Australia , mostly in the south, suggesting a movement into New Zealand from Southern Australia (Smirnov & Timms, 1983).
The cladoceran zooplankton of New Zealand lakes generally contains relatively few species. There are only three common Cladocera: Bosmina meridionalis, Daphnia carinata, and Ceriodaphnia dubia (Stout, 1975b).

Recently, Ceriodaphnia pulchella has been described from some North Island lakes (Greenwood, 1991). Daphnia is less widely distributed than Bosmina and Ceriodaphnia and occurs more frequently in ponds than in lakes (Chapman & Green, 1987). The latter two taxa are common in a variety of lakes, which indicates that these taxa can tolerate a wide range of combinations of biotic and abiotic factors (Burns, 1991).

The faunal elements in the Australasian Cladocera include cosmopolitan genera and species (e.g. Alona spp., Chydorus, and Simocephalus spp.), a small number of endemic Australasian genera (e.g. Saycia, Neothrix, and Pseudomoina) and some endemic Australasian species (e.g. Camptocercus australis, Echinisca schauinslandi, and Moina australiensis). There are also some Gondwanaland species, which are exclusive to the southern continents, and these include Alona cambouei and Leydigia australis (Forsyth & Lewis, 1987). The distribution of Daphnia carinata also can be interpreted as Gondwanan or Lemurian, but with a recent extension from India into China and south-east Asia (Benzie, 1986, 1987).

In the Chydoridae, 12 genera are found throughout New Zealand (Chapman & Lewis, 1976), but the classification of some of the species is not clear. Species of Cladocera have been considered to have broad geographic ranges because of the easy passive dispersal by means of the resting eggs and because a single female can initiate a new population. But Frey (1982, 1987) has pointed out that the suggested cosmopolitanism of many species might not be correct and that further taxonomic work may reveal some species living within a very limited geographic region. This has been shown especially for Chydorus sphaericus. This species was previously thought of as the most widespread and abundant taxon of the Cladocera but is now known to be a complex of probably many species (Frey, 1982, 1987). Frey (1991) recently described Pleuroxus hastirostris and P. helvenacus from the South Island of New Zealand. Neither of the two New Zealand species of Pleuroxus occur in Australia and no species of this genus from other continents are present. Therefore Frey (1991) suggested that there is a much higher degree of endemism in Australasia than was previously thought. Pleuroxus hastirostris was also described by Deevey (1955) from fossil material found in the lake sediments of the Upper Swamp deposits in Pyramid Valley. Exoskeletal components and ephippia of

this species constituted the major part of the fossil cladoceran remains in the deposits. The only other species continuously present (but in much lower numbers) were Daphnia and Simocephalus, which were represented by fossil ephippia. Chydorus, Alonella excisa and Bosmina remains were extremely rare in these sediments and only one specimen was found of each of these taxa.

6.3.1. Taxonomy of the Fossil Cladocera Taxa

The most common fossils of the Chydoridae are head shields, carapaces and postabdomens; whereas Daphniidae leave ephippial eggs and claws, and Bosminidae head shields and carapaces. The fossil Cladocera were identified with reference to Scourfield & Harding, 1958; Frey, 1959, 1991; Flössner, 1972; Chapman & Lewis, 1976; Smirnov & Timms, 1983; Pennak, 1989.

Microphotographs of the exoskeletal components of most of the fossil Cladocera taxa found in the core are presented in Appendix I (Fig. X to XVI) and are referred to in the following section.

Bosmina meridionalis (Fig. X.- A, B, C).
Only head shields and carapaces have been found of B. meridionalis. In this species, the posterior edge of the carapace is practically straight. Mucrones are short as in Fig. X.-B or can be slender with one or several dorsal serrations, and tapering sharply towards the end as in Fig. X.-C (Smirnov and Timms, 1983).

Daphnia sp. (Fig. X.- D).
Ephippia of Daphnia have two parallel-placed eggs. Some fossils consisted of the shelled out inner coverings of the eggs, but Fig. X.-D shows a complete specimen. The ephippium from Lake Grasmere resembles the outline drawing of an ephippium presented by Deevey (1955). Deevey (1955) suggested that the ephippia found in Pyramid Valley might belong to D. carinata (the only described species in New Zealand) because the long axes of the eggs are sub-parallel to the dorsal margin, rather then vertical to it. This is characteristic for the D. magna group to which D. carinata belongs. The ephippia from Lake Grasmere show the same configuration of the egg axes and can

therefore be considered to belong to D. carinata.

Simocephalus sp. (Fig. X.- E, F).
The ephippia of Simocephalus are of a type in which the egg is partly surrounded by a band of hollow cells. Fig. X.-E agrees in its shape with the outline drawing of a Simocephalus ephippium found in Pyramid Valley (Deevey, 1955) in that both have the form of an isosceles triangle. Deevey (1955) suggested that his specimen belonged to S. obtusatus after a comparison with ephippia from an Australian species. Fig. X.-F appears to be slightly different from Fig. X.-E) but this might be due to the partial destruction of the ring of cells surrounding the egg. Stark (1981) recorded S. vetulus in the present-day fauna from Lake Grasmere, but ephippia of this species are shaped more like a scalene triangle so that the fossils from the Lake Grasmere core do not appear to belong to S. vetulus.

Pleuroxus hastirostris (Fig. XI.- G, H, I, J, K).
The carapace is longer than it is high, there is a single small but distinct tooth at the ventro-posterior corner, the ventral margin bulges slightly anterior to middle and the carapace has 8 or 9 short faint striae which parallel the anterior margin. The ventral margin carries feathered setae. The carapace pictured in Fig. XI.-K is unusual in that the striae are repeated from the anterior to the posterior margin. The rostrum is pointed and it is slightly longer than in the head shield depicted by Frey (1991) for this species. The head pores are typical of the subfamily (Fig. XI.-H). The postabdomen is similar to that described by Frey (1991). It has 10 long, slender denticles and most of them have accessory setae associated with them. There is a single row of spinular crescents laterally along the dorsal margin but in the fossil postabdomen from Lake Grasmere additional groups can be found proximally and in the pre-anal region. The claws have two basal spines of which the distal one is approximately the double length of the proximal spine (Fig. XI.-I).

Alonella cf. excisa (Fig. XI.- L, M).
This species has not as yet been recorded from New Zealand (Chapman & Lewis, 1976) and living animals have not been found in any of the author's collections. The fossil New Zealand specimens have the characteristic carapace of A. excisa with striated polygons and

bearing blunt indentations on the posterior edge just above the ventro-posterior corner (Smirnow & Timms, 1983). The head shield (Fig. XI.-L) has prominent longitudinal striae, two median pores, which are widely separated, with the posterior and smaller one close to the margin. Fossil postabdomens were not found in the sediments of the core.

Camptocercus australis (Fig. XII.- N, O, P).
This species has a characteristically drawn-out carapace. The ventro-posterior corner of the carapace is rounded and lacks denticles. The head shield is keeled and therefore seen from the side in microscopic preparations. The fossil head shields from Lake Grasmere are not truncated at the posterior end as in most species of Camptocercus, but are shaped more as in Acroperus. Frey (1958) found a fossil population with similar shaped head shields from Fox Prairie, Indiana. The postabdomen is very long and slender bearing 18 denticles and lateral setae (Fig. XII.-P).

Graptoleberis testudinaria (Fig. XII.- Q, R).
The carapace and head shield of this species are very distinctive. The carapace has a characteristic reticulation with mostly two (rarely three) prominent upturned teeth at the posterior-ventral angle. The head shield is reticulate all over, the rostrum is broadly rounded, and there are three head pores connected by a narrow channel. The lateral pores are prominent because of the tube-like thickening of the chitin (Frey, 1958).

Monospilus dispar (Fig. XII.- S, T, U).
The carapace of Monospilus is nearly round with a conspicuous reticulation. The carapace pictured (Fig. XII.-T) is that of a first instar animal. Later instar carapaces would have concentric growth lines because this species does not shed the old carapaces with each moulting. The postabdomen is short and broad with seven marginal denticles and numerous clusters of fine lateral setae. The head shield has only one head pore and multiple scallops on the tip of the rostrum. Frey (pers. com.) suggested that this morphological character might denote a new species, although only M. dispar has been recognized world-wide. Smirnov and Timms (1983) recorded two possibly new species from Australia. The New Zealand specimens differ from both

Australian forms. M. elongatus has an oblong carapace and an elongated postabdomen bearing differently arranged setae as to those on the postabdomen of M. dispar; and M. diporus has two head pores, and a postabdomen with only four denticles and a small number of lateral clusters of setae.

Chydorus sp. (Fig. XIII.- A, B, C, E, F, G).
It was not possible to designate a species name for the fossil material although it resembles Chydorus sphaericus. C. sphaericus was considered to be present and widespread in New Zealand, but studies by Frey (1980) have shown that the so-called taxonomic unit is highly variable and contains at least two species groups. Species belonging to these two groups will be different in different parts of the world and it is likely that the animals which have been called Chydorus sphaericus in New Zealand will be a new species.

The carapace of the fossil material is broadly elliptical bearing a faint reticulate pattern. The dorsal margin is short relative to the length of the carapace. The ventro-posterior angle is well developed and without teeth. In the head shield the posterior portion is longer than the rostrum and is rounded narrowly at its end. The rostrum is short and tapered usually being slightly emarginate. There are two major head pores situated in the median part of the head shield. Postabdomens were only found in association with carapaces. The only part to be preserved was the distal third of the ventral margin and the denticle bearing dorsal margin and the claws. The claws have two basal spines. The dorsal edge of the postabdomen is armed with about 10 (?) denticles.

Biapertura affinis (Fig. XIV.- H, I, J, K, L).
This species has a posteriorly pointed head shield (a type which occurs only in B. affinis and A. quadrangularis), which is longer and narrower than that of A. quadrangularis, and possesses two median head pores connected by a narrow channel. The two smaller lateral pores are usually joined to the main channel by chitinized thickenings of the head shield (Frey, 1958), which give the appearance of fine lines (Fig. XIV.-H). The carapace has a sharp notch dorsally (Fig. XIV. - I,J) indicating that a pointed head shield fits in there. The ventral margin is only slightly convex and carries along its whole length

feathered setae which are longer towards the anterior end. The carapace is patterned with fine, closely spaced longitudinal striae, which are irregular and sometimes interrupted. The postabdomen of the female (Fig. XIV.-L) has 14 anal denticles and a single row of groups of lateral setae. The postabdomen of the male (Fig. XIV.-K) narrows distally and bears lateral groups of setae, but is without the anal denticles.

Biapertura setigera (Fig. XIV.- M, N).
The carapace of this species is as high as it is wide, the ventro-posterior corner is rounded without a tooth, and the ventral margin is nearly straight. The carapace has faint longitudinal striae. The head shield has a short rounded rostrum. There are two major head pores connected by a narrow channel. The lateral head pores are elongated and obvious. The postabdomen is short and broad with a straight, slightly tapering ventral edge, truncated at the distal edge and angled, with the longest denticle positioned at the angle formed by the distal and dorsal margin. The dorsal margin carries 12 anal denticles, the postabdominal claw has one basal spine.

Alona quadrangularis (Fig. XV.- O, P, Q, R, S, T, U).
As in B. affinis, this species has a posteriorly pointed head shield but with three median head pores connected by a narrow channel. Generally, the lateral pores are inconspicuous as in Fig. XV.-O. The head shield depicted in Fig. V.-P and Q shows some aberration in the shape of the head pores in that two of the median pores have disappeared, and the lateral pores are relatively conspicuous and apparently connected to the remainder of the median channel by a chitinized thickening of the shell. A small number of such head shields have been found in the fossil material from Lake Grasmere. Frey (pers. com.) found similar fossil A. quadrangularis head shields in sediments from Schleinsee in Germany, in which the three median head pores had disappeared in all possible combinations. Similar aberrations have not been found in B. affinis (Frey, pers. com.). The carapace of A. quadrangularis generally has only longitudinal striae and is finely and densely granulated ("dicht gekörnt", Flössner, 1972). The postabdomen in the female (Fig. XV.-U) is distally widened with 17 denticles at its dorsal margin and with a single row of groups of lateral setae. The postabdomen in the male (Fig. XV.-S) is without

anal denticles but with a lateral row of groups of setae.

Alona cf. rectangula (Fig. XVI.- V, W, X, Y).
The carapace of the fossil material is evenly arched and bears striae (the pattern is similar to that pictured for A. rectangula novae-zealandiae in Smirnov and Timms (1983)), and the ventral edge is slightly convex. Around its posterior ventral corner a row of fine marginal spinules is positioned. This row starts anteriorly to the posterior ventral angle, where the long ventral setae end, and continues around the angle for a short distance. The marginal spinules then take up a submarginal position. The marginal spinules are regarded by Frey (1958) as morphologically characteristic for this species. The head shield has three small pores connected by a very narrow channel. The head shield is broad and short, with a blunt rostrum. The posterior portion which attaches to the carapace is wider than the rostrum. The postabdomen is short and in the male (Fig. XVI.-X) lacks the marginal teeth but carries well developed lateral setae. The female postabdomen (Fig. XVI.-Y(?)) carries about 13 denticles and lateral setae. The number of denticles is higher than described in the literature, e.g. Flössner (1972) gave 7-10 denticles for the postabdomen of A. rectangula. The identification of this taxon is somewhat uncertain because there are a number of subspecies in Australasia whose taxonomic situation is not clear. Furthermore, live animals have not been found for comparison with the fossil material.

Ilyocryptus spp.
Only the very characteristic carapace of this taxon has been found in low numbers. The carapace can be recognized by its fringe of long, branched setae on the ventral and posterior edge. Concentric bands on the carapace are derived from old exuvia which stay attached to the new integument at each moult (Chapman & Lewis, 1976).

6.4. Results

The number of Cladocera remains in samples from the Lake Grasmere core (Fig. 6.1.) showed marked fluctuations. The first Cladocera remains were found at the 322 cm horizon (derived from the basal clay/silt layer) in very low numbers (23 exuviae per ml of sediment). In the following samples, the number of cladoceran microfossils increased but in the older sediments of the core, below 150 cm, number of Cladocera remains were generally low. A pronounced minimum was recorded in the 200 cm sample from which only 8 exoskeleton components were retrieved. The number of Cladocera fossils increased considerably in the 150 cm sample, remained high in the sediment layers between 150 and 60 cm, and decreased to a second minimum at the 40 cm horizon (93 remains). Above that sediment horizon Cladocera microfossils increased again and reached the highest occurrence in the core at the 20 cm horizon (7675 fossils per ml of sediment). In the following sample the number of cladoceran fossils showed a marked decline to a relatively low number in the 12 cm sample. In the most recent sediments, the occurrence of Cladocera remains increased again to reach a second maximum in the top sample.

In the sediment core from Lake Grasmere, 14 Cladocera species have been distinguished in the fossil fauna (Table 6.1.). Of these species, 12 are benthic and inhabit the littoral zone and two belong to planktic forms. The ratio of planktic to littoral Cladocera is presented in Fig. 6.1. Generally, more planktic Cladocera occurred during the last 6000 years of Lake Grasmere's history, although several periods are indicated in which the relationship was reversed. Especially in the older sediments, below 200 cm, the ratio of planktic to littoral forms fluctuated strongly. From 322 cm up to 295 cm, benthic Cladocera were dominant in the fossil assemblages (with one exception at the 318 cm horizon). In the following sediment layers up to 195 cm changes in the dominance of benthic or planktic forms were following each other rapidly. From 180 cm up to the top of the core planktic Cladocera were prevalent in the fossil assemblages except for two short periods represented by the 50 and 40 cm samples and the 25 cm sample, in which benthic Cladocera were dominant.

Fig. 6.1. Lake Grasmere: Summary figure illustrating the total number of Cladocera remains, the ratio of planktonic to littoral Cladocera, and the number of taxa in the samples from the core.

Table 6.1. Lake Grasmere: Fossil Cladocera Taxa and Additional Present-day Chydoridae Taxa (* - taxon found in present-day collections by the author, ** - new record for Lake Grasmere).

Bosmina meridionalis (Sars, 1904)		
Daphnia sp.		
Simocephalus sp.		
Chydoridae		
Alona quadrangularis (Müller, 1784)		
Alona cf. *rectangula*		
Biapertura affinis (Leydig, 1860)		**
Biapertura setigera (Brehm, 1931)		**
Graptoleberis testudinaria (Fisher, 1851)	*	
Monospilus dispar (Sars, 1862)		
Camptocercus australis (Sars, 1896)		**
Alonella cf. *excisa*		
Chydorus sp.	*	
Pleuroxus hastirostris (Sars, 1903)		
Macrothricidae		
Ilyocryptus sp.		
Only found in recent collections by the author:		
Alona cf. *guttata*		
Leydigia sp.		

The number of taxa in the samples ranged from five taxa in the 322 cm sample to 13 taxa in the 50 cm sample (Fig. 6.1.). But in most samples throughout the core nine to 11 taxa occurred. In the samples derived from the layer in the core which contained the Grana minora particles (204 to 195 cm), only six to seven taxa were recorded in the fossil Cladocera material.

Amongst the 14 species identified in the Lake Grasmere core (Table 6.1.) were two planktic species, Bosmina meridionalis and Daphnia sp. Species of Simocephalus, although belonging to the Daphniidae, live mostly in the littoral zone of lakes amongst rooted vegetation. The animals can swim but only short distances. Mostly they are substrate bound and can attach themselves to macrophytes with the help of a curved bristle at the outer edge of the antennae (Flössner, 1972).

Chydoridae were represented by ten species and one species was found belonging to the Macrothricidae (Ilyocryptus sp.).

The stratigraphy of the relative abundances of the fossil Cladocera taxa throughout the core is presented in Fig. 6.2. (in which the percentages of the taxa were calculated from the total sum of fossils) and in Fig. 6.3., in which only the relative abundances of the Chydoridae are presented (percentages calculated from the total sum of the Chydoridae fossils). Bosmina (Fig. 6.2) was the most abundant taxon in the fossil assemblages throughout most of the core. In the older sediments below 180 cm the relative abundances of Bosmina were generally lower and fluctuated markedly. In the basal clay/silt layer, Bosmina was found in a low relative abundance in the 322 cm sample, but its abundance increased to a temporary maximum in the 319 cm sample, and then declined to its lowest relative abundance in the core in the sediments between 313 and 295 cm. Above that level the relative abundance of Bosmina increased again declining to lower abundances only at the 247 and 200 cm horizons. Above 180 cm up to the top of the core, the relative abundance of this taxon remained high and stable with the exception of one marked decline in the 40 cm sample, which began in the 60 cm sample.

Daphnia ephippia were found continuously in relatively low abundances throughout the pre-Polynesian period, and this taxon disappeared from the fossil fauna at the 50 cm level. Daphnia had its maximum abundance in the oldest organically rich sediments between 313 and 295 cm. Simocephalus ephippia occurred only sporadically in the fossil fauna and Ilyocryptus (not included in the figures) was also rare and appeared mostly in low numbers in the youngest sediments (see Appendix, Table II.4.).

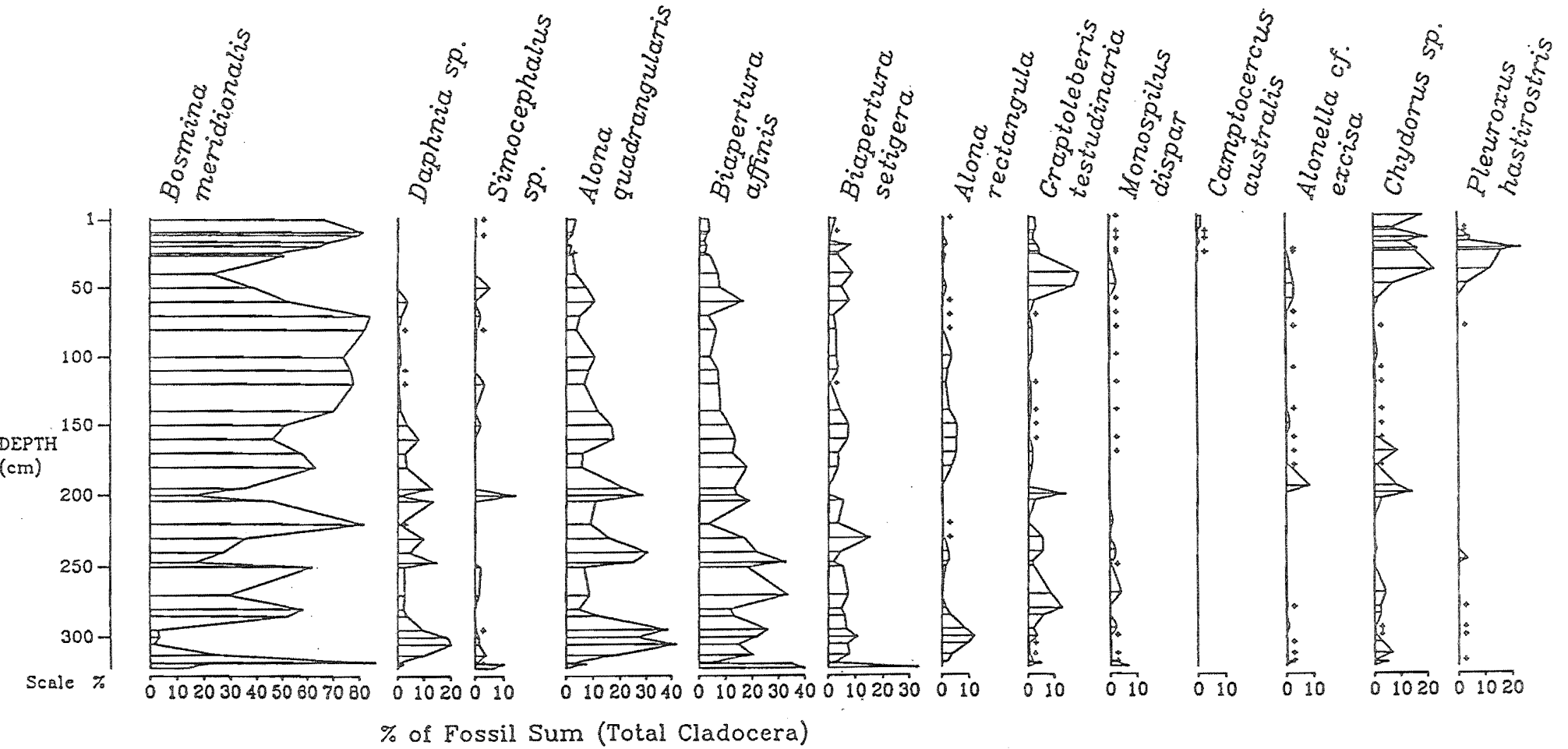


Fig. 6.2. Lake Grasmere: Percentage diagram of fossil Cladocera in the core (percentages are calculated as proportions of the fossil sum at each sampling level).

In the fossil Chydoridae fauna (Fig. 6.3.) Biapertura affinis and Alona quadrangularis were clearly the dominant components. The relative abundance of B. affinis was high in the oldest samples from the core but declined slightly in the sediment layer between 318 and 280 cm. During this time the relative abundance of A. quadrangularis increased and this species had its maximum occurrence at the 305 cm level. Above 285 cm, the proportion of A. quadrangularis decreased, whereas that of B. affinis increased considerably. The proportion of the latter species remained relatively high and stable above the 240 cm horizon with only slight minima in the 220, 200, 160, and 100 cm samples. In the youngest sediments (above 50 cm), the relative abundance of B. affinis was low in most samples. The distribution of A. quadrangularis above 247 cm showed only minor fluctuations, but in the youngest sediments the relative abundance of this taxon was low, similar to that of B. affinis.

Biapertura setigera occurred throughout the core with a relatively stable abundance. This taxon was not found in the 195, 200 and 17 cm sample and its abundance was generally lower in the youngest sediments. A. cf. rectangula was slightly more abundant in the oldest organically rich sediments and in the sediment layer between 180 and 50 cm. The relative abundance of Graptoleberis testudinaria was higher in the younger sediments with a maximum in the 40 and 50 cm samples. This taxon had only one single peak abundance in the older sediments at the 270 cm horizon. Monospilus dispar and Alonella cf. excisa were not common in the fossil assemblages, but M. dispar was slightly more abundant in the older sediments, whereas A. cf. excisa became slightly more abundant above the 200 cm level. Camptocercus australis possibly invaded Lake Grasmere only recently and appeared for the first time in the 27 cm sample.

Chydorus sp. was not an abundant component of the fossil fauna below the 50 cm level except for two higher relative abundances at the 200 and 170 cm level. Above the 50 cm horizon, this taxon became the dominant fossil chydorid. Pleuroxus hastirostris was rare in the core below 50 cm, but became the sub-dominant chydorid in the sediment layer between 40 an 12 cm. In the most recent sediments the proportion of this taxon declined and it did not occur in the top sample.

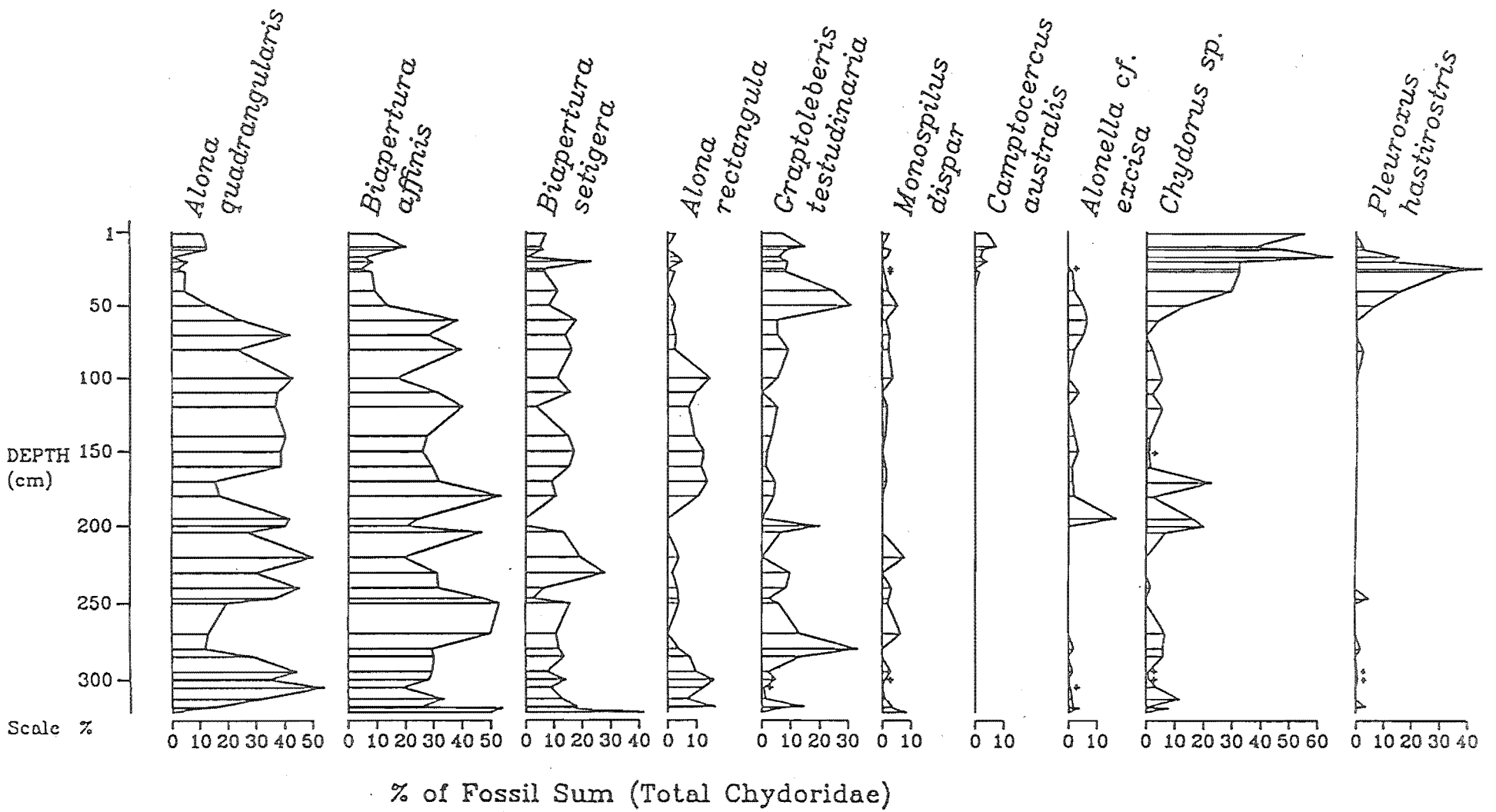


Fig. 6.3. Lake Grasmere: Percentage diagram of fossil Chydoridae in the core (percentages are calculated as proportions of the sum of fossil Chydoridae remains in each sample).

To summarize, of the 14 fossil Cladocera taxa present in the Lake Grasmere core, Bosmina was the dominant form for most of the period covered by the core. Biapertura affinis and Alona quadrangularis were more important in the older sediments, whereas Chydorus and Pleuroxus became the dominant Chydoridae in the youngest sediments (in the Polynesian and European periods).

6.4.1. Numerical Analyses

The community structure of the fossil Cladocera fauna through time was analysed by using a classification analysis and an ordination technique (correspondence analysis) on the samples from the core (see Chapter II). The data matrix for the numerical analyses consisted of the percentage abundances of the 14 Cladocera taxa in 38 samples.

The hierarchical cluster analysis was based on the percentage similarity of community (PSc-index). The classification was made as group average clustering of the samples and the results are presented in Fig. 6.4. Four distinct sediment groups were formed by the cluster analysis and one sample (322 cm) was classified as an outlier. The groups consisted of the following sediment sequences (the sample numbers in brackets refer to the numbering of the samples in the correspondence analysis):

Group I: 1 to 20 cm (samples 1 - 5), 70 to 140 cm (samples 11 - 16), 220 cm (sample 24), and 318 cm (sample 36);
Group II: 25 to 50 cm (samples 6 - 9);
Group III: 60 cm (sample 10), 150 to 180 cm (samples 17 - 20), 204 cm (sample 23), 250 cm (sample 28), 280 to 285 cm (samples 30, 31);
Group IV: 195 to 200 cm (samples 21, 22), 230 to 247 cm (samples 25 - 27), 270 cm (sample 29), 295 to 313 cm (samples 32 - 35), 319 cm (sample 37).

The results of the cluster analysis indicate vertical changes in the composition of the fossil Cladocera fauna but the sediment sequences do not follow the time series of the samples in the core. Furthermore, the groups are only partly homogeneous indicating considerable changes in the composition in the fossil fauna in relatively short time

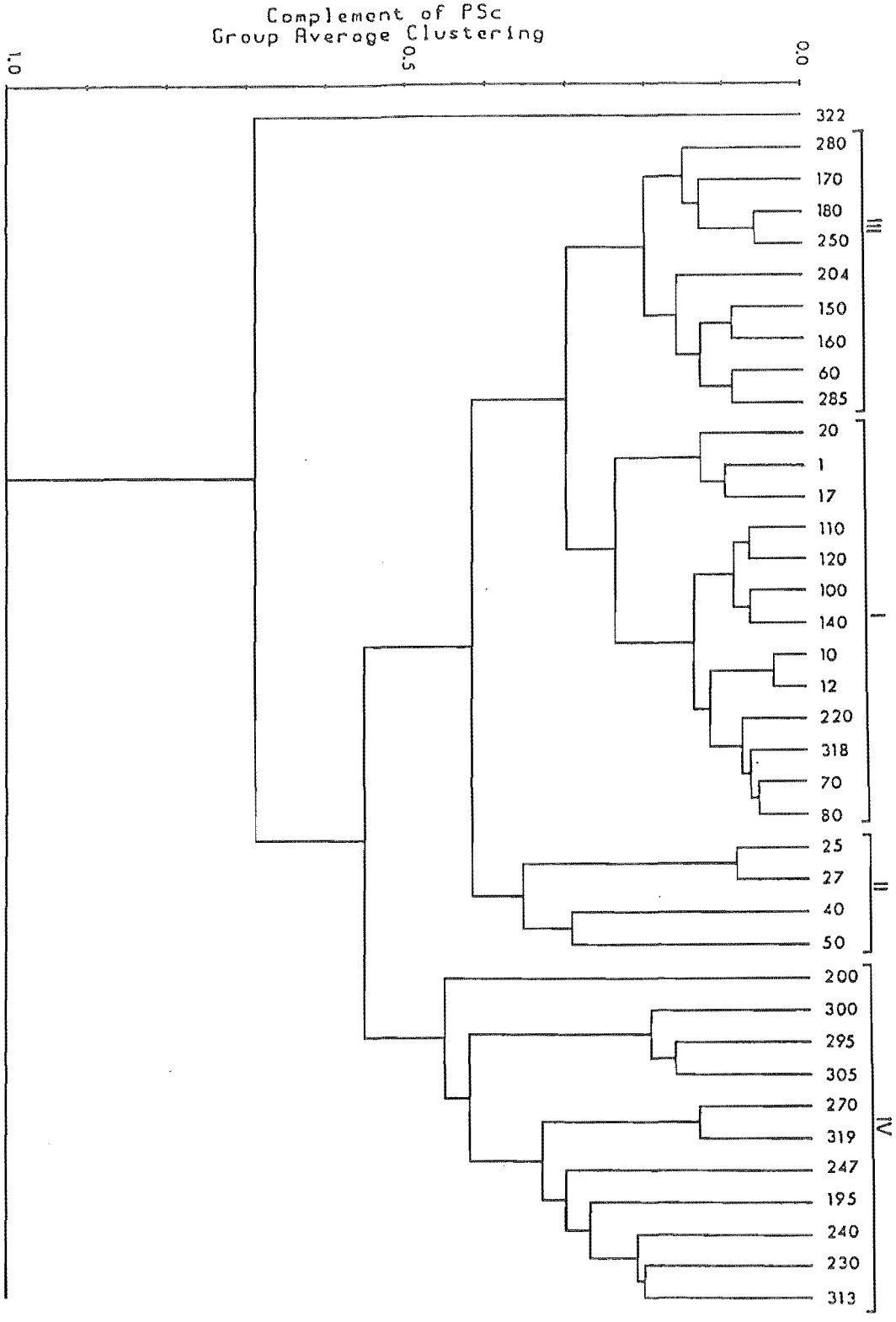


Fig. 6.4. Lake Grasmere: Dendrogram based on an average linkage cluster analysis on the relative abundance of the fossil Cladocera taxa in the samples from the core. The vertical axis gives the values of the dissimilarity index. The group codes are indicated by Roman numerals.

intervals. Group I consists mostly of the younger sediments interrupted by the sediment sequence of group II. Some samples of group III are following group I in age (150 to 180 cm); and group IV, which contains most of the oldest sediments below 195 cm, is disrupted by single samples or pairs of samples belonging to the first three sediment groups. The 322 cm sample (38) has been classified as an outlier because of high relative abundances of B. affinis (40%) and B. setigera (33.3%).

In Table 6.2., the mean relative abundances of the fossil Cladocera taxa (of all samples in one group) are related to the sample clusters. The division of sample clusters on the basis of changes in the faunal composition is clearly shown for all groups and was based on the following faunal components: Group I had the highest abundance of Bosmina and generally low abundances of the remaining Cladocera, except for Alona quadrangularis and Chydorus; Group II had a relatively low abundance of Bosmina, abundances of Chydorus, Pleuroxus

Table 6.2. Lake Grasmere: Two-way table of coincidence giving the mean relative abundances (%) of the fossil Cladocera taxa in each sample cluster (Groups I-IV), N = number of samples in each group.

TAXON/GROUP	I	II	III	IV
Bosmina meridionalis	76.1	40.1	53.5	25.1
Daphnia sp.	1.2	0.0	5.3	9.9
Simocephalus sp.	0.6	1.3	0.2	3.2
Alona quadrangularis	5.2	3.6	10.5	24.5
Alona cf. *rectangula*	1.2	0.7	3.1	3.8
Biapertura affinis	4.4	5.2	14.4	24.5
Biapertura setigera	2.6	5.0	5.6	6.6
Graptoleberis testudinaria	1.5	11.2	3.6	4.5
Monospilus dispar	0.5	1.4	0.2	1.4
Camptocercus australis	0.5	0.2	0.1	0.0
Alonella cf. *excisa*	0.2	1.5	0.9	1.3
Chydorus sp.	5.4	15.8	2.5	4.1
Pleuroxus hastirostris	0.8	14.0	0.1	0.4
Ilyocryptus sp.	0.3	0.2	0.0	0.0
N	13	4	8	11

and Graptoleberis were high, and those of the other taxa low; in Group III, the relative abundance of Bosmina was higher than in group II and IV, but not as high as in group I, and the relative abundances of Alona quadrangularis and Biapertura affinis had increased, as well as that of Daphnia, whereas the relative abundances of Chydorus and Pleuroxus were at their minimum; and in group IV, Bosmina had its lowest relative abundance, but Daphnia, A. quadrangularis and B. affinis had their maximum occurrences in the core.

In the ordination analysis the samples are represented by points in a two-dimensional ordination diagram (Fig. 6.5.). The ordination diagram is based on the sample scores for the first two axes. The canonical correlation R (Orlóci, 1978) was R(X/Y)=0.5632 for Set 1 and R(X/Y)=0.4332 for Set 2.

The groupings of the sediment sequences derived from the clustering of the samples were corroborated by the results of the ordination analysis. Samples of group I have high scores on axis one and the lowest scores on axis two. These samples were dominated by Bosmina. The division of group I into two sub-groups is due to the occurrence of Chydorus in the samples 1 to 5, but not in the remaining samples of this group (70 - 140 cm). Samples of group II had lower scores on axis one and higher scores on axis two than had group I. These samples were dominated by Chydorus, Pleuroxus, and Graptoleberis. Group III is also placed in the lower right quadrant with group I, but has lower scores on axis one and higher scores on axis two than the latter sediment group. These samples also had high abundances of Bosmina, and those of A. quadrangularis and B. affinis were increasing. Samples of group IV were nearly all placed in the two left-handed quadrants with low scores on axis two and even lower scores on axis one. The three samples with the lowest scores on axis one (32 - 34, 305, 300, and 295 cm) had fossil assemblages with the lowest relative abundances of Bosmina in the core (1.4 to 3.6% of the total fossils) and the maximum relative abundances of A. quadrangularis (25.9 - 41.2%).

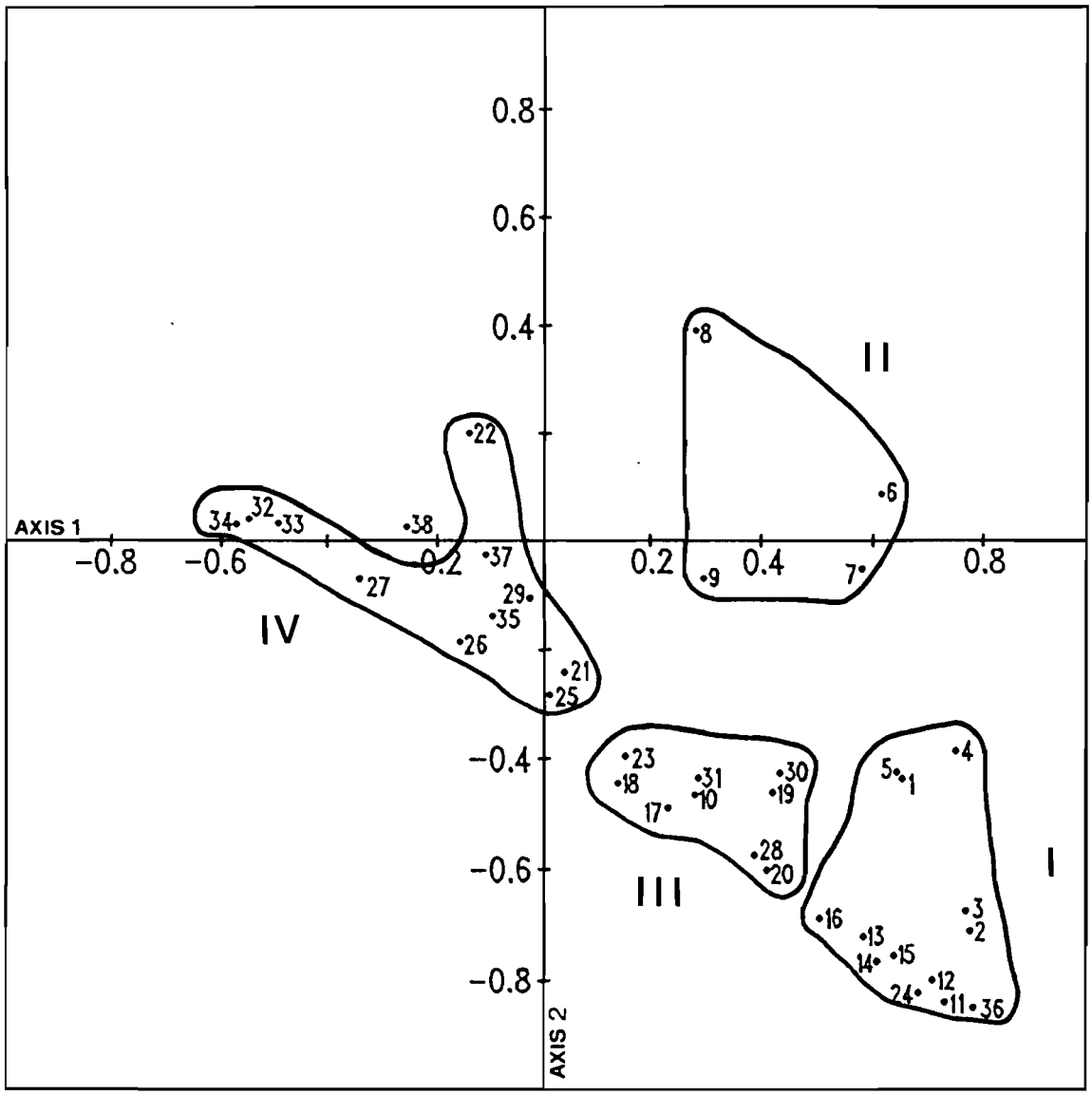


Fig. 6.5. Lake Grasmere: Reciprocal averaging ordination of samples from the core based on the relative abundance of fossil Cladocera taxa.

6.5. Discussion

The stratigraphy of the Cladocera remains in the sediment profile from Lake Grasmere indicate that, during the last 6000 years of the lake's history, the fossil fauna did not remain stable but showed marked fluctuations and changes in community structure and number of deposited remains. In discussing these changes, two main questions are of interest: is the development of the fossil cladoceran fauna a reflection of changing conditions in the lake or its catchment? And are the inferences, derived from the fossil Cladocera, consistent with those derived from the other parameters studied in the core, e.g. fossil diatoms, chironomids and plant pigments?

6.5.1. Comparison of the composition of the fossil and recent cladoceran fauna in Lake Grasmere

The fossil fauna from Lake Grasmere comprised 14 taxa, whereas Stark (1981) recorded nine taxa in the recent fauna collected in the macrophyte zone of the lake. Two of the latter taxa are planktic forms, Bosmina meridionalis and Ceriodaphnia dubia, and these two taxa constitute the sole true limnetic Cladocera species recorded in present-day collections (Stout, 1969, 1991). Bosmina was also present in the fossil fauna but ephippia of Ceriodaphnia have not been found in the core samples. That does not necessarily mean that Ceriodaphnia did not occur in the lake during the last 6000 years. Ephippial females of this species are not common and have been found only in a limited number of lakes (Chapman & Green, 1987) although these lakes included Lake Grasmere. In a detailed study of Ceriodaphnia in this lake, ephippial females were observed in low numbers only transiently at times of peak population numbers in summer (Staples, 1984). It is likely that the numbers of ephippia produced were insufficient to be found in the small sample volumes from the core. It also might be possible that this taxon represents a more recent invasion of Lake Grasmere as was found for Camptocercus australis.

Of the remaining taxa, Ilyocryptus, Simocephalus (but possibly two different species), Graptoleberis testudinaria, and Chydorus (?) sphaericus were recorded in both the fossil and present-day fauna. The

latter two taxa were also found in present-day collections by the author (unpubl. data, Chydorus sp. was found on 11 Jan. 1989, and Graptoleberis testudinaria on 5 Dec. 1988).

Three taxa recorded by Stark (1981) have not been found in the fossil fauna: Leydigia (?) australis, Alona guttata and Neothrix armata. The latter species belongs to the Macrothricidae and is therefore not likely to leave remains in sediments. Alona cf. guttata and Leydigia sp. were also collected by the author (unpubl. data, Alona cf. guttata was found on 5 Dec. 1988, Leydigia sp. on 11 Jan. 1989) in samples of macrophyte fragments washed up at the south-eastern shore of Lake Grasmere. These two taxa might be recent invaders of the lake, or have only recently increased in abundance through changes in some conditions of the lake (e.g. changes in trophic state), which might have produced more favourable conditions for them. Another possibility is that they might live in a habitat so close to the shoreline that their remains are rarely transported into the deeper part of the lake. Stark (1981, Appendix 2) recorded A. guttata in higher numbers at sampling sites with water depths between 0-1 m, e.g. collected amongst Isoetes at the western, eastern and southern sides of the lake, and amongst Myriophyllum at the southern side of the lake.

Taxa which were not recorded by Stark (1981), but occurred in the fossil fauna, included Biapertura affinis, B. setigera, and Camptocercus australis. These species have been found by the author in present-day collections from Lake Grasmere (unpubl. data, B. affinis was found on 1 Feb. 1989, B. setigera and C. australis on 5 Dec. 1988). These species raise the number of recorded Cladocera species for Lake Grasmere from nine to 12 species.

Five chydorid taxa were found only in the fossil fauna. These include Alona quadrangularis, A. cf. rectangula, Alonella cf. excisa, Monospilus dispar, and Pleuroxus hastirostris. It would be of interest to study surficial sediment samples from Lake Grasmere to determine whether the latter species do occur in the more recent fauna. Overall, the fossil cladoceran fauna appears to agree with the living community relatively well with the exception of possibly Ceriodaphnia, and two chydorid taxa (Leydigia sp. and A. cf. guttata).

The species number of 10 taxa in the fossil chydorid fauna in Lake Grasmere represents a rather depauperate fauna in comparison with other Holocene chydorid communities, especially from some lakes in the northern hemisphere. In northern Germany, Frey (1958) found 16 chydorid species in an extinct lake at Wallensen, Hofmann (1978, 1986b) found 25 taxa in the Segeberger See, and 27 Chydoridae in both the Grosser Plöner See and Schöhsee. The fossil chydorid fauna of Belham Tarn (England) consisted of 17 taxa (Harmsworth, 1968), that of Blèdowo Lake (Poland) of 22 chydorids (Szeroczyńska, 1991), and in Mirror Lake (New Hampshire) 28 species were found (Goulden & Vostreys, 1985). A low species number similar to that in Lake Grasmere has been recorded only from more extreme environments, e.g. lakes at high elevation. The fossil chydorid fauna of Lac du Bouchet (France) was composed of only 11 species (Hofmann, 1991) and that of Lago Cadagno (Southern Switzerland) of 12 chydorids (Boucherle & Züllig, 1988). An alpine lake on mainland Australia, Blue Lake, had a fossil chydorid assemblage of only eight species (see Chapter IX, section 9.2.7.2.). The above mentioned examples show that the overall species diversity of the Cladocera in Lake Grasmere appears to be rather low as has been found for other invertebrate groups in New Zealand (Forsyth & Lewis, 1987).

6.5.2. Core stratigraphy of the fossil Cladocera

Ecological information about present-day Cladocera taxa in New Zealand which could be used for interpretation of the core stratigraphy of the fossil Cladocera, is rather sparse. This is true especially for the Chydoridae, and the information available includes mainly descriptions of the distribution of chydorid taxa in freshwaters in New Zealand (Stout, 1975a,b; Winterbourn & Lewis, 1975; Chapman & Lewis, 1976; Crumpton, 1978; Burns et al., 1984). Even in the case of the possibly cosmopolitan species, it does not necessarily follow that the New Zealand species have the same ecological requirements as the same species in other parts of the world. Therefore, the interpretation of the fossil cladoceran fauna from Lake Grasmere has to be without consideration of detailed ecological factors, which might have influenced or controlled the temporal distribution of the fossil fauna, and instead will be concerned with broader aspects of the past limnology of Lake Grasmere.

As was established earlier (see Chapters III and V), no major change in macroclimate occurred during the last 6000 years covered by the sedimentary record. Changes in the composition of the fossil cladoceran community are therefore not caused by major climatic changes, but may have been caused mainly by the amount of minerogenous matter entering the lake, changes in water depth and the availability of food and/or lake productivity.

In the 322 cm sample, derived from the basal clay/silt of the core, cladoceran remains were extremely rare (23 remains) and only five taxa were distinguished. The high input of minerogenous matter into the lake during this time, which caused highly turbid waters, would have been responsible for the very low deposition rate of cladoceran remains (Whiteside & Swindoll, 1988). Similar occurrences were found by Boucherle and Züllig (1988) in Lago Cadagno, Southern Switzerland, where high inputs of allochthonous material caused by landslides or avalanches, reduced not only the number of remains, but also the species diversity, and the concentration of other organic remains. Because of the elimination of nearly all organic remains caused by these events, Boucherle and Züllig (1988) argued that short-termed disturbances were responsible and not erosion, which would have occurred more slowly and would not have obliterated all remains. This same reasoning might be valid for the event influencing Lake Grasmere 6000 years ago. It was suggested (see Chapter III) that the cause of the high input of clay and silt might have been a high magnitude storm resulting in high sediment loads of an inflowing river. The initial input appeared to have eliminated most of the fauna (e.g. the chironomids and the Cladocera at 326 cm) and after that the fauna recovered in a time span whose duration is not known, while the turbidity ceased through settling of the suspensoids. The very low fossil density in the 322 cm sample also might have been caused partly by dilution of remains through a relatively high sedimentation rate. Although the highest relative abundances in the 322 cm sample were recorded for Biapertura affinis and B. setigera, which are littoral species, it appears that initially the limnetic Bosmina was more successful in recolonizing the lake. From a relative abundance of 13.3% in the 322 cm sample, this taxon increased in numbers of remains in the following two samples and accounted for 85% of the fossil community at the 318 cm horizon. It is possible that, although lake

waters were clearing and therefore enabling Bosmina to survive, the littoral areas of Lake Grasmere were still to some degree unsuitable for chydorids (e.g. not providing sufficient macrophytes or detritus) for some time. The peak in relative abundance of Bosmina was an isolated occurrence in the oldest sediments and in the next sample (313 cm) the relative abundance of this taxon declined to 26.4% (Fig. 6.2.), and in the sediment layer above declined to its lowest occurrence in the core.

The first episode of decreased concentration of fossil Cladocera in the core was followed later in the developmental history of Lake Grasmere by several similar events, which also caused a reduction in cladoceran remains and diversity, but differed in magnitude and duration. These are represented in the core by the sediment layers 270 to 195 cm, 50 to 40 cm and 17 to 12 cm (Fig.s 6.1. and 6.2.). These sediments are characterized by relatively low contents of water and loss-on-ignition pointing to an increased input of minerogenous matter. The ratio of planktic to littoral Cladocera in these samples was in most of these instances very low indicating that, although both littoral and planktic Cladocera reacted negatively to higher turbidity as was shown by the reduction of remains, the decrease of planktic forms was comparatively greater. The ratio of planktic to littoral Cladocera can indicate the relative amount of open water versus the littoral area. But as the low fossil densities in those sediment layers are probably caused by an increase of allochthonous matter, the actual cause for the low ratios might be somewhat obscured. It is possible that the low ratios do not reflect changes of the water level during all of these periods.

Bosmina meridionalis is the most common limnetic cladoceran in New Zealand and occurs in most types of lakes, e.g. it was recorded amongst the dominant zooplankton in the large glacial lakes in the South Island, in the Waitaki hydro-electric lakes, and in the smaller Canterbury lakes (Stout, 1975b). This taxon is very rare or excluded from small and shallow water bodies. In ponds near Lake Tekapo, Burns et al. (1984) recorded Bosmina in low abundances in only a very small number of the ponds studied, Crumpton (1978) did not find Bosmina in the South Island ponds studied by her, and in the pond studies listed by Stout (1975b), Bosmina was not recorded. In Pyramid Valley, Deevey

(1955) found only one exuvium of Bosmina in the extinct lake, which was probably small and shallow. Therefore, the amount of open water present in a water body appears to be one of the controlling factors of the abundance of Bosmina, so that the planktic/littoral ratio in cores might give some information about changes in water depth or the relative amount of the littoral area. Turbidity appears to have a negative effect on Bosmina. In Lake Grasmere, numbers of Bosmina were low at times of greatest turbidity in late winter (Stout, 1991), when temperatures and food levels were also lowered. Koenings et al. (1990) have found that the mechanism by which filter-feeding cladocerans (e.g. Bosmina and Daphnia) are excluded from turbid glacier-meltwater lakes in Alaska appears to be "the energetically costly increase in filtering and feeding rates necessary to overcome the insufficient energy extractable from ingested foods mixed with silt" (Koenings et al., 1990, p. 65). These effects are mediated in freshwater environments with higher temperatures because of increased algal biomass, the colonization of land-derived silt by bacteria as well as the adsorption of energy-rich organics to these particles (Arruda et al., 1983).

Besides factors such as water depth and turbidity, zooplankton communities are mainly regulated in population size by food availability. Invertebrate predators or planktivorous fish have not shown any obvious impact on zooplankton communities in New Zealand (Chapman & Green, 1985). Only very few studies on zooplankton have included observations of the gut contents. Burns (1979) found that the identifiable gut contents of Bosmina meridionalis from Lake Hayes consisted mainly of Oocystis and Cyclotella.

The sediment layer 270 to 195 cm, although characterized by a generally low fossil density, includes two environmental disturbances which left recognisable layers in the core lithography (see Chapter III): a dark layer between 260 and 258 cm and the layer containing sand particles (204-200 cm). The latter sediment layer might have been deposited by a short-termed event (e.g. an earthquake) causing the highest magnitude of disturbance. The 200 cm sample contained the minimum number of remains (8 exoskeletal components) which correlated with a minimum in the content of organic matter in this sample (Fig. 3.3. and Appendix, Table II.1). In the first sample above the sandy

layer (195 cm), numbers of remains increased only slightly (as did the amount of organic matter deposited in this sample) possibly indicating that even though a short-termed event might have been responsible for the reduction of the fauna, the recovery of the fossil fauna needed some time.

In the sediments below the sandy layer, two isolated peak abundances of fossil remains were found, in the 250 cm and especially in the 220 cm sample. The higher numbers of remains were mainly due to an increase in Bosmina fossils, which dominated the fauna (81.6% relative abundance) causing a high planktic/littoral ratio. The dominance of a limnetic cladoceran in these samples might point to a rise in water level during these periods. This was corroborated by the profiles of fossil diatoms in the core. The increase of Cyclotella and the decline of Fragilaria at the 240 cm horizon indicated a rise in water level (which were marked especially at the 220 cm level, Fig.s 3.4. and 3.5.), and the distribution of these diatom taxa in the core above that layer pointed to possible fluctuations of the water level during most of Lake Grasmere's history. An increase in the abundance of Cyclotella would have also provided more food matter for Bosmina.

Two more periods of low fossil deposition were recorded in the core. In the sediments between 50 and 40 cm only a minor decline in organic matter and water content was found, but the responsible event had a considerable impact on the fossil community. The number of cladoceran remains in the 40 cm sample was reduced to 93 exoskeletal components (of which only 22.2% belonged to Bosmina), and also the numbers of fossil diatoms and chironomids were greatly reduced (see Section 3.8. and Chapter V). The cause of the disturbance at this time is unknown, but it might have been related to activities connected to the New Ribbonwood Fan (e.g. a possible encroachment of the fan, see Chapter III). The latest disturbance in the youngest sediments (17-10 cm) was of a lesser magnitude in terms of the reduction of fossil numbers. During this period the planktic/littoral ratio remained high indicating either no decrease in water level or that the littoral area was more influenced affecting the habitats of the Chydoridae. The disturbance causing the latest decline in fossil number might have been related to the arrival of the Polynesian people.

In the core the number of cladoceran remains was generally lower in the older sediments. After the deposition of the sandy layer and the recovery phase of the fossil fauna (above 195 cm), the number of deposited remains increased quickly in the following samples and at the 150 cm horizon a five-fold increase was found (Fig. 6.1.), which was caused mainly by higher abundances of Bosmina (Fig. 6.2.). This taxon remained dominant throughout the entire period up to the 60 cm level with only a slightly fluctuating planktic/littoral ratio. This sediment layer represented the longest stable period in the history of Lake Grasmere during the last 6000 years. The high relative abundance of Bosmina indicated open water conditions and an increase in lake productivity. Bosmina belongs to the dominant forms of the zooplankton in mesotrophic and eutrophic lakes (Stout, 1975b), where it might be favoured by higher food availability. A slight increase in lake productivity was also indicated by the increased amounts of organic matter in these sediments. Fossil diatom numbers were highest during this time and the profiles in the core of the major diatom taxa indicated a relatively high but fluctuating water level (see section 3.8.). There might have been an isolated pulse of nutrients into the lake at the beginning of this period. Stephanodiscus, a diatom characteristic of eutrophic lakes, was found only at the 140 cm horizon in a slightly increased relative abundance (Fig. 3.5.) but was extremely rare in other samples from the core. The higher numbers of diatoms, and especially of Cyclotella, during this period would have provided the necessary food supply for the increase of the population size of Bosmina as represented by the higher number of deposited remains in the sediments.

In the youngest sediments (50 cm to the top of the core) numbers of cladoceran fossils remained generally high (with the exception of the already described disturbances). Although the maximum number of fossils was recorded at the 20 cm horizon, the relative abundances of Bosmina were not as high in this and adjacent samples as in the sediments between 150 and 60 cm, but increased towards the top of the core. Between 27 and 20 cm, the planktic/littoral ratio was relatively low pointing to a possible temporary lowering of the lake level. This was corroborated by a short-termed decline in this period in the relative abundance of Cyclotella (Fig. 3.5.), and the maximum abundance of Orthocladiinae sp. IX indicating a possible increased

macrophyte cover (Fig. 5.2.). In the top sediments, the relative abundance of Bosmina increased again indicating a higher water level (as was shown by the diatom stratigraphy as well (Fig. 3.4.) and possibly an increase in the trophic conditions of the lake waters.

In summary, the distribution of Bosmina in the core indicated an expansion of open water conditions above the 250 cm horizon by relatively high abundances of this taxon in the following sediment layers: in some samples between 250 and 220 cm, between 180 to 60cm, and in the youngest sediments. This could have been due to a rise in water level (Goulden & Vostreys, 1985). In sediment layers with increased input of minerogenous matter the abundances of Bosmina were reduced.

The distribution of the littoral taxa (Fig. 6.3.) showed that four taxa, Alona quadrangularis, A. cf. rectangula, Biapertura affinis and B. setigera, were generally more abundant in the older sediments of the core, below 50 cm, and occurred above that level in only low relative abundances. Three taxa, which were rare in the older sediments became dominant above the 50 cm horizon: Graptoleberis testudinaria, Pleuroxus hastirostris and Chydorus sp.

All these species are crawling or creeping species living in the littoral zone either close to macrophytes or associated with filamentous algae. Chydorus may appear in the plankton attached to filamentous algae. Not much is known about their specific ecology and it is therefore impossible at this point in time to determine the factor(s) which have caused the distinct shift in the dominance pattern of the fossil chydorid assemblage.

In the older sediments, A. quadrangularis and B. affinis were the most abundant chydorids. During the period which is represented by the oldest organically rich sediments, A. quadrangularis was dominant and B. affinis was the sub-dominant species. The relative abundance of Bosmina was minimal and the planktic/littoral ratio indicated an extended area of the littoral zone. Nothing is known about the ecology of A. quadrangularis in New Zealand. This species was recorded in low numbers from ponds near Lakes Tekapo and Ohau (Burns et al., 1984). B. affinis has been found living on detritus around the base of plants

(Chapman & Lewis, 1976), and amongst the filamentous algae covering the pebbles on the south-eastern shore of Lake Grasmere by the author. Crumpton (1978) recorded this species from Hukarere and Shipley's ponds. Both ponds had extensive beds of macrophytes and filamentous algae were abundant amongst the rooted vegetation during the summer months. The presence of B. affinis and possibly A. quadrangularis therefore might be indicative of shallow waters and the presence of macrophytes. The diatom flora in the sediment layer between 313 and 295 cm also indicated a shallow lake with abundant macrophytes (Fig. 3.4.). Furthermore, Bosmina occurred with the lowest relative abundances during this period which also indicated shallow water.

Above the oldest organically rich sediments, when lowered contents of organic matter in the sediments pointed to a relatively high input of minerogenous matter, the proportion of these species amongst the chydorid fauna in the samples remained high but showed some fluctuations indicating the continued presence of macrophytes in the lake, but an increasing reduction of the littoral zone through time. This became more obvious in the sediments between 150 and 60 cm, in which the planktic/littoral ratio had maximum values.

Above the 50 cm level, Graptoleberis, Pleuroxus, and Chydorus became the most abundant chydorids in the fossil assemblage. All three taxa were found in the sediments between 50 and 30 cm, the period of an environmental disturbance, and were apparently less influenced by it than other taxa. According to the diatom stratigraphy (Fig. 3.4.), the water level remained possibly high below the 30 cm horizon and fell only between 30 and 20 cm. It is unlikely that the lake then would have become as shallow as it had been during the time the oldest organic sediments were deposited, when the proportion of Fragilaria in the fossil diatom flora was higher (see Fig. 3.5.). The presence of Pleuroxus during the time of the disturbance and the following period of possibly increased macrophyte cover (as was indicated by Orthocladiinae sp. IX) and its subsequent disappearance in the most recent sediments is difficult to explain. This species is considered to prefer the smaller bodies of water (Chapman & Lewis, 1976). It was the most abundant chydorid in the extinct lake in Pyramid Valley and occurred together with Corynocera (Deevey, 1955). In Lake Grasmere Pleuroxus became abundant after Corynocera probably had disappeared

from the lake (above the 50 cm horizon).

Graptoleberis is a relatively common species in New Zealand and is found amongst aquatic plants. It lives on the leaves and stems, scraping off bacteria from their surfaces (Chapman & Lewis, 1976). This species has been recorded from the ponds near Lakes Tekapo and Ohau (Burns et al., 1984) and by Stark (1981) in most of his sampling stations in Lake Grasmere. It occurred in highest numbers in the Elodea beds at the western side of the lake down to a water depth of 4 m.

Thus, both species appear to be associated with macrophytes and Pleuroxus reached its maximum occurrence in the sediment layer when Orthocladiinae sp. IX was dominant. But during this period (30-20 cm) the relative abundance of Graptoleberis had already declined and remained relatively low up to the top of the core. This distribution of Graptoleberis is difficult to understand especially considering its present-day occurrence in Lake Grasmere. Although, there is the possibility that Graptoleberis became again more abundant in Lake Grasmere after the introduction of Elodea to the lake whose now extensive beds could have provided this species with an increased area of habitat.

The species which became dominant in the chydorid assemblage above the 50 cm level and remained so up to the top of the core was Chydorus sp. This taxon is the most common chydorid in New Zealand and has been recorded by Stark (1981) for Lake Grasmere, by Burns et al. (1984) for many of the ponds studied, and by Crumpton (1978). In the ponds studied by her, Chydorus was especially abundant in the shallow weed beds. This species is considered to be part of the 'aufwuchs' of the littoral zone of lakes and its appearance might be related to the presence of filamentous algae, which form the substrate for it to cling to (Winterbourn & Lewis, 1975). This species also has been regarded as an indicator for eutrophication when it occurs in the plankton associated with blue-green algae blooms (Winterbourn & Lewis, 1978). Its relatively high abundances in the younger sediments might have been related firstly to the increased macrophyte cover (30-20 cm) and then to a slightly increased trophic state in the top sediments, in which Chironomus became dominant (see Chapter V). Increasing

abundances of Chironomus may be the result of a higher trophic state of lake waters. The factors which limited the growth of A. quadrangularis and B. affinis in the younger sediments are not known.

Daphnia has never been recorded from present-day Lake Grasmere. In the core, it has been found in the older sediments below the 50 cm horizon but disappeared from the fossil assemblage above that level. Daphnia had its maximum occurrence during the initial shallow phase of the lake, when A. quadrangularis and B. affinis were dominant. This distribution agrees somewhat with the present-day distribution of Daphnia. This taxon is more frequently found in ponds than in lakes especially in the South Island (Chapman & Green, 1985). The abundance of Daphnia is apparently not strongly controlled by predation but instead by food availability. But Chapman and Green (1985) argued that there have to be other factors (as yet unknown) limiting the occurrence of Daphnia because it did not occur in some lakes in which conditions were apparently favourable for this taxon. In the core, numbers of ephippia from Daphnia were low during times of increased turbidity or environmental disturbances. When the lake level was possibly higher (between 150 and 60 cm), the relative abundance of Daphnia became very low. The cause for the disappearance of Daphnia at the 50 cm horizon in the core is not known.

The classification analysis separated groups of sediment samples according to the proportion of littoral or planktic species in the samples (Fig. 6.4.). A similar result was derived from the ordination analysis (Fig. 6.5.). The environmental gradient, on which the samples have been ordered, expressed on axis one might be interpreted as water depth. Shallower waters (samples with the highest proportion of A. quadrangularis and B. affinis) are represented by low scores on axis one; and higher water levels (samples with the highest proportion of Bosmina) are represented with high scores on axis one. It is not known which environmental gradient is represented on axis two. There are higher scores on axis two when Bosmina is accompanied in the samples by Chydorus, Pleuroxus and Graptoleberis, but lower scores, when the samples contain high proportions of Bosmina and Chydorus, and lowest scores on axis two, when samples contain the highest relative abundances of Bosmina and only moderate proportions of A. quadrangularis and B. affinis.

To conclude, the stratigraphy of the fossil Cladocera from the Lake Grasmere core showed two major trends: the Cladocera fauna reacted negatively to increased mineral input and the fauna alternated between a community dominated by planktic forms and one dominated by littoral species. More research is needed on the biology and taxonomy especially of the Chydoridae. This information would be useful for the interpretation of the distribution of the fossil taxa in sediment cores. This study has shown that there is a good correlation with the profiles of different organic remains in the core from Lake Grasmere indicating that the information derived from the fossil Cladocera about conditions in the past of Lake Grasmere is consistent with that derived from the other parameters.

6.6. Summary

In the fossil Cladocera fauna from the Lake Grasmere core, 14 species were distinguished. Two species were planktic and ten species belonged to the benthic Chydoridae. Several factors influenced the composition of the fossil Cladocera fauna including the amount of minerogenous matter, changes in water depth, food availability and lake productivity. Increased mineral influx into the lake caused by high magnitude storms or earthquakes resulted in sudden decreases in the quantities of Cladocera remains. At the time of some of these events, sedimentation was increased so strongly that the remains were rare due to dilution by allochthonous material. Increased turbidity prevailing over a longer time interval also caused a negative response of the fauna reducing especially the number of remains of planktic forms. Changes in lake levels caused the fauna to alternate between communities dominated by planktic forms (mainly Bosmina meridionalis) and communities dominated by benthic species. During the initial low lake level phase, represented in the core by the oldest organically rich sediments of the core, Alona quadrangularis and Biapertura affinis were dominant; whereas in the younger sediments, during a short-term period of increased macrophyte cover and a possible lowering of the lake level, Chydorus sp. and Pleuroxus hastirostris were dominant. Relatively higher lake productivity, when coupled with higher water levels above the 160 cm horizon in the core and greater availability of food for the zooplankton, caused a marked increase in the abundance of cladoceran remains, particularly of Bosmina remains.

CHAPTER VII

FOSSIL PIGMENTS

7.1. Introduction

The analysis of fossil plant pigments preserved in lacustrine sediments has been used as a palaeolimnological technique since the pioneering studies by Vallentyne (1955, 1956), Gorham (1960, 1961), and Fogg and Belcher (1961). Sedimentary pigments provide information on productivity changes within a given lake during its past history and can be used to differentiate between autochthonous and allochthonous origins of contributions to the lake (Swain, 1985; Sanger, 1988).

The fossil pigment fraction of sediments is derived autochthonously from decaying organisms which have lived within the lake, and from allochthonous material such as leaves from trees, shrubs, and shoreline plants. Smaller amounts of pigments originate from soil humus layers and peat, from where they are eroded in small particles and transported into the lake via inflows or surface run-off. The pigments which arrive at the mud surface, and are subsequently incorporated in the sediments, are almost exclusively chlorophylls and carotenoids. These pigments are water insoluble and membrane bound. Water soluble pigments such as anthocyanins and phycobilins are usually destroyed prior to deposition in sediments (Sanger & Gorham, 1970). Pigments reach the sediment in various stages of degradation depending on the time the pigment bearing particles spent in the water column and the degree of chemical and organism attack. Pigments are best preserved when intact cells are deposited with membrane complexes and chloroplastids still enclosed within cell walls. But it is more common that cell and membrane structures are disrupted by passage through the guts of the zooplankton and the benthic fauna. Pigments survive ingestion but are usually excreted in partially decomposed forms such as isomers, allomers, and fragmented pieces of the original molecule (Daley, 1973; Daley & Brown, 1973).

Amongst the chlorophylls, chlorophyll *a* is the most abundant pigment in all major groups of freshwater photosynthetic organisms and forms several degradation products which are well preserved in sediments. These are: chlorophyll *a'*, a tautomer of chlorophyll *a*; pheophytin *a*, formed by removal of the magnesium atom from either chlorophyll; and pheophorbide *a*, which lacks both magnesium and the phytol chain of the chlorophyll molecule (Carpenter & Bergquist, 1985). In sediments, a mixture of native undegraded chlorophyll and the various degradation products is found. Degradation pathways are influenced by a variety of factors in the sedimentary environment so that it is difficult to determine why a particular product is present. The degradation of chlorophyll *a* appears to continue after burial in the sediments with time (Sanger, 1988), but pheophytin *a* concentrations relative to total organic carbon remain the same over time (Daley & Brown, 1973). To reduce these problems, chlorophyll derivatives are measured as total sedimentary chlorophyll degradation products (SCDP or CD) and are expressed as SCDP per unit of sedimentary organic matter.

Carotenoids are universally present in lake sediments (Züllig, 1981, 1982, 1989). They are found in all photosynthetic organisms including cyanophytes and photosynthetic bacteria. Carotenoids are bound to membrane complexes of prokaryotic cells adjacent to chlorophyll molecules, and in higher plants they occur similarly in chloroplastids as well as in the non-chlorophyllous chromoplastids (Goodwin, 1980). Carotenoids occur as hydrocarbon carotenes (the most common being β-carotene) and oxygenated xanthophylls (the most abundant being lutein, violaxanthin, neoxanthin, cryptoxanthin, and zeaxanthin). Once buried in the sediments, carotenoids are very stable, and if decomposition occurs it is similar to that of organic matter as a whole (Sanger, 1988). For example, Vallentyne (1960) found carotenoids in 20,000 year old sediments from Searles; and Watts et al. (1977) described the occurrence of carotenoids in 5000 to 340,000 year old marine sediments. When analysing carotenoids from lake sediments, it is possible to differentiate between the various carotenoid pigments. In this thesis however, only the concentration of total carotenoids has been measured.

The concentrations of chlorophyll derivatives and carotenoids incorporated into permanent sediments are applied as palaeoindicators

of productivity changes within a lake. Many studies have found positive correlations between profundal pigment concentrations of surface sediments and indices of modern primary production (Gorham et al., 1974; Guilizzoni et al., 1983) and it has been suggested that variations in preserved pigments from cores might display a record of past trophic levels. However, there is no obvious reason that a productive lake should produce more pigment per gram organic matter than should an unproductive lake. The explanation for the higher concentration of fossil pigments in eutrophic lakes is thought to be the lesser degradation of autochthonous pigments relative to their organic matrix, and the lesser dilution by pigment-poor allochthonous organic matter in eutrophic lakes. In less productive lakes, the greater light intensity and hypolimnetic oxygen concentration promote degradation and pigment-poor allochthonous organics constitute a greater proportion of the sedimentary organic matter (Sanger & Gorham, 1972). Factors believed to enhance preservation of pigments include low temperatures of the waters at the bottom of lakes, as well as anoxic conditions, high sedimentation rates, and absence of benthic organisms in sediments. Factors which promote low pigment concentrations are high light penetration and long exposure times to oxidation between the time of death of the organism and burial beneath the surface oxidizing zone, and sediment resuspension of shallow water sediments containing low pigment concentration (Sanger, 1988).

Pigments can be expressed as ratios of each other (e.g. chlorophyll derivatives (CD) to total carotenoids (TC)). The advantage of using ratios is that potentially misleading variables are eliminated in the calculation; the variables in the ratio serve as controls for each other. The use of ratios of pigments can obviate such factors as variation in sediment accumulation rate (Swain, 1985). Low values of chlorophyll to carotenoids ratios are generally found in eutrophic lakes, whereas oligotrophic lakes yield high ratios (Gorham & Sanger, 1975). The higher ratios in oligotrophic lakes are partly caused by the faster degradation of carotenoids than chlorophylls in oxidizing conditions, as can be found in soil humus layers or oxidized microzones of bottom sediments in oligotrophic lakes. The reducing conditions found in sediments of stratified eutrophic lakes preserve both chorophylls and carotenoids at levels near to those at production, therefore producing low CD/TC ratios. The ratio is also

influenced by the amount of allochthonous input with low concentrations of plant pigments which can dilute the autochthonously produced pigments in the sediments. Swain (1985) noted that the low ratios in eutrophic lakes can also result from the changed concentrations of chlorophylls and carotenoids produced in the lake.

Recent studies of sedimentary pigments have attempted to establish relationships between production, degradation, and sedimentation of plant pigments in lakes (Carpenter et al., 1986; Leavitt & Carpenter, 1990a; Hurley & Armstrong, 1991), monitored the effects of changes in the composition of the zooplankton fauna on algal communities and subsequently the composition of the deposited pigments in sediments (Carpenter & Bergquist, 1985; Leavitt & Brown, 1988; Leavitt et al., 1989; Leavitt & Carpenter, 1990b; Carpenter & Leavitt, 1991) and investigated sources of variability in pigment concentrations in surface sediments of lakes (Hilton et al., 1991).

In New Zealand, the analysis of fossil pigments was included in studies of short sediment cores from Lake Rotorua (Rawlence, 1984) and Lake Rotoiti (Rawlence, 1985) in the North Island to establish whether the eruption of Mt. Tarawera in 1886 immediately increased the trophic status of the lakes. In both lakes, the concentration of sedimentary pigments increased gradually over the post-eruptive period, with no obvious evidence of any increase resulting directly from the eruption. Relatively low values of fossil pigments in a core from Lake Maratoto, North Island, covering the last 17,000 years of the lake's history, revealed that the lake remained unproductive throughout its history. Changes in the water level of Lake Maratoto in the past, and changes in the balance betweeen autochthonous and allochthonous sources of organic matter were also indicated by the fossil pigment profiles from Lake Maratoto (Green, 1979; Green & Lowe, 1985).

In the present study, fossil pigments in samples from the Lake Grasmere core have been investigated with the objective to gain information about productivity changes in the past of the lake and to establish the influence which allochthonous input had on the lake. The stratigraphy of the sedimentary plant pigments will be compared (see Chapter X) with the those of the other organic remains to establish possible correlations between changes in the sedimentary parameters.

7.2. Methods

The determination of fossil pigments in samples from the Lake Grasmere core was carried out according to the method described by Bengtson and Enell (1986). The frozen sediment samples (see Chapter 2.1.) were thawed and 1 ml of the wet sediment of each sample was used for the analysis. All steps of the operation were carried out as much as possible in the dark or near dark. The pigments were extracted as follows: 1 ml of sediment was homogenized with 5 ml of 90 % acetone, the suspension was then centrifuged and the supernatant decanted into a 50 ml volumetric flask. The extraction of pigments was repeated three times on the remaining precipitant. The collected supernatant was diluted to 50 ml with 90% acetone, well mixed, and then transferred to a gas-tight jar. The jar was covered with aluminium foil to keep the sample in the dark and stored at 4°C until the measurement of the pigments was carried out. The chlorophyll derivatives were determined spectrophotometrically in the acetone extract at the 665 nm absorbance peak for chlorophylls. 90% acetone was used as a blank.

For the separation of the carotenoid bearing phase of the extract, 25 ml of the remaining acetone extract were mixed with 20% methylalcoholic potassium hydroxide in a 250 ml flask and shaken on a shaking table in the dark for two hours at room temperature. The solution was then transferred to a separating funnel and 25 ml petroleum ether and 25 ml distilled water were added to it. The mixture was shaken vigorously for 2 minutes. After separation, the water phase was discarded, and the petroleum ether phase was washed with 25 ml distilled water. The water phase as well as the first 10 ml of the petroleum ether phase were then discarded, and the remaining petroleum ether extract was transferred to a gas-tight jar. The jar was stored in the dark at 4°C until determination of the carotenoids. The carotenoids were determined spectrophotometrically in the petroleum ether extract at 450 nm. Petroleum ether was used as a blank.

The pigment concentrations in the extracts were expressed as spectrophotometric units (PU) per gram of organic matter. One unit is equivalent to an absorbance of 0.1 in a 1 cm quartz cuvette when dissolved in 100 ml of solvent. The pigment units were calculated using the following formula (Bengtson & Enell, 1986):

$$\text{Pigment units (PU)} = \frac{10 \times (\text{abs-x} - \text{abs-0}) \times \text{V-extr.}}{(\text{V-x} \times \text{BD} \times \text{DW} \times \text{IG}) \times 100 \times \text{cell}}$$

where abs-x = absorbance of sample
abs-0 = absorbance of blank
V-extr. = volume of acetone extract (50 ml)
V-x = volume of sample (1 ml)
BD = density of samples (g/ml)
DW = dry weight of sample (g/g)
IG = loss on ignition of sample (g/g DW)
V-x. x D x DW x IG = organic matter (g)
cell = length of the cuvette

The sediment parameters were analysed from sediment samples parallel to the fossil pigment samples as described in Chapter 2.1. The calculations of the sediment parameters for the fossil pigment analysis were carried out as follows (Bengtson & Enell, 1986):

$$\text{Bulk density BD} = \frac{B - A}{\text{ml of sample}} \text{ g/ml}$$

$$\text{Dry weight DW} = \frac{C - A}{B - A} \text{ g/g}$$

$$\text{Loss on ignition IG} = \frac{C - D}{B - A} \text{ g/g}$$

where A = weight of the crucible (g), B = weight of the wet sample + crucible, C = weight of dried sample + crucible, D = weight of ash + crucible.

7.3. Results

Fossil pigments were analysed from 28 sediment samples from the Lake Grasmere core, as well as from two surface sediment samples from Lake Grasmere taken at a water depth of 9 m and 12 m respectively. The calculated pigment units for chlorophyll derivatives and total carotenoids, and the values for the ratio chlorophyll derivatives to total carotenoids are given in Table 7.1. Fig. 7.1. presents the profiles of the pigments and the pigment ratio for the Lake Grasmere cor51Xwith the

fluctuations in the carotenoid stratigraphy being more pronounced than those of the chlorophylls.

The chlorophyll concentration was initially low in a sample taken from the clay/silt layer at the base of the core (see Fig. 3.2.) and increased sharply to relatively high values in the 317 and 301 cm samples. In the samples above the 301 cm horizon the concentrations of chlorophylls decreased to a minimum concentration in the 258 cm sample. In the next two samples, at 225 and 215 cm, the chlorophyll concentrations increased, but then declined sharply to the lowest content of chlorophylls in the 198 cm sample. Above that horizon the chlorophyll concentrations increased again and remained high until the 65 cm level with a maximum in the 85 cm sample. This is the highest concentration of chlorophyll derivatives found in the core. Above the 65 cm horizon, chlorophyll values in the samples decreased to a minimum at the 45 cm and 10 cm sample with slight maxima of chlorophyll concentrations in the 20 cm sample and in the top sample of the core.

The stratigraphy of the total carotenoid concentrations displayed nearly the same pattern as the chlorophyll profile. Very low concentrations of carotenoids were found at the base of the core, in the 258 cm sample, at the 198 cm horizon, and in the samples at 35 and 10 cm. Relatively high concentrations of carotenoids were found in the 301 cm sample, in the sediment layers between 175 and 75 cm with the maximum in this layer at 85 cm, and at the 20 cm horizon and in the

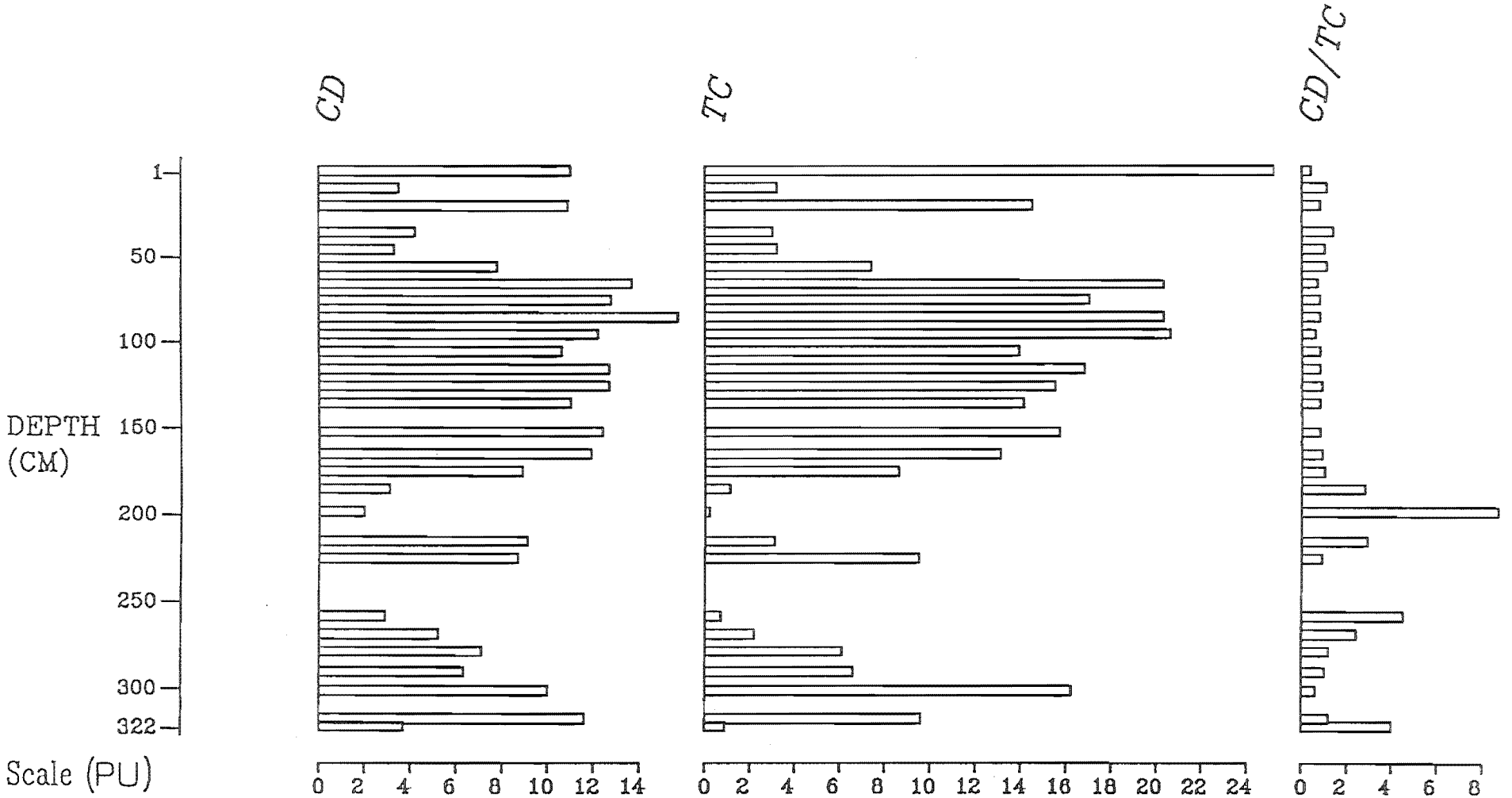


Fig. 7.1. Lake Grasmere: Profiles of Chlorophyll Derivatives (CD), Total Carotenoids (TC), and the CD/TC ratio in the core. Pigment concentrations are given as spectrophotometric units (PU - for definition see Table 7.1.).

top sample. The latter sample contained the highest carotenoid concentration in the core.

The recent pigment concentrations analysed from surficial sediment samples were considerably higher for both pigment types than the pigment concentrations reached in the core samples (Table 7.1.). Chlorophyll derivatives and total carotenoids had maximum concentrations in the sample which was taken at the shallower site at a water depth of 9 m.

The ratio of chlorophyll derivatives to total carotenoids changed markedly throughout the core. Values ranged from 0.44 in the top sample of the core to 8.7 at the 198 cm horizon (Table 7.1.). The initially high CD/TC ratio in the basal sample decreased to a minimum value at the 301 cm level and rose in the above sediment layers to a relatively high value in the 258 cm sample, decreased to a value below 1.0 in the 225 cm sample, and then rose to the maximum of 8.7 at the 198 cm level. In the next two samples, the ratio CD/TC decreased and remained relatively constant in the section of the core between 265 and 65 cm. In the younger sediments the ratio fluctuated around 1.0 and decreased to the smallest value at the top of the core. The values for the ratio of chlorophyll derivatives to carotenoids in the surficial sediment samples were slightly higher than the CD/TC ratio of the top sample with the smaller value being found in the sample at 9 m water depth.

In summary, the distribution of the two parameters, chlorophyll derivatives and total carotenoids, and the ratio of the two pigment types exhibited three major phases: in the lower portion of the core (from the basal sediments up to 175 cm) and also in the younger sediments (from 55 cm to the top of the core) the pigment concentrations as well as the CD/TC ratio showed great irregularities and abrupt changes. In the zone of the core between 165 and 65 cm, pigment concentrations were high and relatively stable, and the ratio remained low (<1.0) and uniform throughout this period.

Table 7.1. Fossil Pigments in sediment samples from the Lake Grasmere core.

Sample (cm)	Absorbance 665nm	450nm	Chlorophyll Derivatives (CD)	Total Carotenoids (TC)	Ratio: CD/TC
1	0.028	0.064	11.0	25.2	0.44
10	0.024	0.022	3.5	3.2	1.08
20	0.063	0.084	10.9	14.5	0.75
35	0.028	0.020	4.2	3.0	1.38
45	0.030	0.029	3.3	3.2	1.03
55	0.041	0.039	7.8	7.4	1.05
65	0.047	0.070	13.7	20.3	0.67
75	0.052	0.069	12.8	17.0	0.75
85	0.058	0.075	15.7	20.3	0.77
95	0.054	0.091	12.2	20.6	0.59
105	0.052	0.068	10.6	13.9	0.76
115	0.055	0.069	12.7	16.8	0.75
125	0.055	0.066	12.7	15.5	0.82
135	0.054	0.068	11.0	14.1	0.78
152	0.060	0.076	12.4	15.7	0.79
165	0.053	0.058	11.9	13.1	0.91
175	0.051	0.049	8.9	8.6	1.03
185	0.026	0.009	3.1	1.1	2.82
198	0.026	0.003	2.0	0.2	8.70
215	0.051	0.017	9.1	3.1	2.94
225	0.050	0.055	8.7	9.5	0.92
258	0.027	0.006	2.9	0.7	4.53
268	0.036	0.015	5.2	2.2	2.36
278	0.044	0.038	7.1	6.1	1.16
290	0.044	0.046	6.3	6.6	0.95
301	0.057	0.092	10.0	16.2	0.62
317	0.070	0.058	11.6	9.6	1.21
321	0.035	0.009	3.7	0.9	3.94
Fossil Pigments in surficial sediment samples from Lake Grasmere (sampling date January 18, 1990, water depth: S12 - 12m at southern end of the lake, N9 - 9m at northern end of the lake).					
S12	0.122	0.144	25.0	29.5	0.85
N9	0.122	0.191	33.11	56.5	0.59

Pigment concentrations are given as spectrophotometric units (PU) per gram of organic matter, one unit being equivalent to an absorbance of 0.1 in a 1 cm quartz cuvette when dissolved in 100 ml of solvent (Bengtsson and Enell, 1986).

7.4. Discussion

When interpreting the stratigraphies of fossil pigments in sediment cores from lacustrine environments, several factors have to be taken into account. It has been shown that primary production is one of the major determinants of fossil pigment concentrations in lake sediments. A greater production rate (at a given time) provides a higher concentration of pigments in the organic matter of the sediment profile (Sanger & Gorham, 1972; Gorham et al.; 1974; Sanger & Crowl, 1979). But pigment deposition rates are also influenced by lake morphology, sedimentation rate and type of deposited material, photodegradation (which is most potent in small, slowly sinking particles), selective grazing (Carpenter et al., 1986; Leavitt et al., 1989)), and sediment focussing (Forbes & Hickman, 1981; Davis et al., 1985b; Hickman, 1987). These factors are important in determining the degree of preservation of pigments in sediments.

In the sediment core from Lake Grasmere, chlorophyll derivatives as well as total carotenoids fluctuated strongly through time. Several periods of relatively high in-lake productivity were indicated alternating with generally shorter periods of either low in-lake productivity or high influx of pigment-poor allochthonous organics.

Periods in which low pigment concentrations per unit of organic matter were deposited in the sediments were represented by the samples 321 cm, 268-258 cm, 198-185 cm, 45-35 cm, and 10 cm (Fig. 7.1.). In most of these samples the concentrations of carotenoids were considerably lower than that of the chlorophyll derivatives resulting in very high CD/TC ratios. This was more pronounced in the older sediments of the core between ca. 6000 and 3000 yr B.P. than in the younger sediments. Extremely low carotenoid concentrations were found in the basal clay/silt layer, in the dark grey lamination discernable from adjacent sediment layers at 260 cm, and the sediments containing the Grana minora particles in the section of the core between 204 and 200 cm. The latter sediments contained the lowest concentrations of both pigment types in the core (Fig. 7.1., Table 7.1.). All sediment layers with high CD/TC ratios exhibited also very low concentrations of organic matter and water content indicating a high input of inorganic material during these periods of deposition.

The high input of very fine minerogenous matter at the basal end of the core represented a major disturbance for the benthic fauna as shown by the absence of remains in the oldest sample of the core (326 cm) and by very low fossil densities of Chironomidae and Chydoridae in later samples. The planktic forms (Bosmina and Daphnia) as well as the diatoms showed a negative response and occurred in very low abundances in samples derived from this layer. During this period, sedimentation would have been rapid, and waters turbid without much in-lake productivity. Presumably the greater part of the small amount of organic matter deposited was allochthonous, with well-oxidized organic matter bearing only small amounts of fossil pigments.

Carotenoids in soils are subject to faster degradation than chlorophylls through a variety of factors (e.g. oxidation, frequent wetting and drying, destruction by animals, bacteria, and fungi). These conditions in soils can decay carotenoids to colourless derivatives and cause the ratios of chlorophylls to carotenoids to be higher in soils than in lake sediments (Sanger, 1988). In lake sediments, high pigment ratios may indicate either high allochthonous input or high aerobic decomposition in the lake (Sanger & Gorham, 1972). In the sediments of the basal layer, the organic matter content was extremely low and, taken together with a very high pigment ratio, allochthonous input of organic matter during this period is indicated.

Sanger and Gorham (1972) found chlorophyll/carotenoids ratios of 5.0 to 15.0 in the uppermost sediment layers of a core from Kirchner Marsh, Minnesota. These sediments were deposited as true swamp peats. They noted that the pigment ratios recorded from these sediments had reached higher levels than any observed before in swamp or bog peats and that some of the low carotenoid concentrations were comparable to those measured in dry woodland soils and in swamp hummocks.

In the Lake Grasmere core, the pigment ratios in the basal layer as well as in the sediments from the 260 cm horizon were very high (3.9 and 4.5 respectively) indicating high allochthonous input. The pigment ratio in the sediments containing the Grana minora particles was unusually high reaching a level of 8.7. Sanger (1971) recorded a pheophytin a : total carotenoids ratio of 7.7 in oak leaves overwintering on the ground. The unusually high ratio in the 204 to

196 cm layer in the Lake Grasmere therefore might point to a largely terrestrial origin of the organic matter. A high input of terrestrial material into the lake might support the view that the deposition of sand in this layer was due to a landslide caused by an earthquake. In New Zealand, earthquakes are recognized for their ability to initiate landslides (Blong & Eyles, 1989). Whitehouse and Griffiths (1983) have shown an observed frequency of landslides with volumes >1 x $10^6 m^3$ of one per 244 years over the last 10,000 years in the Southern Alps. The authors considered that most of these landslides were triggered by earthquakes. An alternative explanation for the input of terrestrial material to the 204 to 196 cm layer could have been a large storm or or a series of storms as mentioned earlier (see Chapter III).

In the younger sediments of the Lake Grasmere core two more phases of low pigment deposition were observed. These phases were represented by the sediment layer between 45-35 cm and by the 10 cm sample. In these sediments chlorophyll derivatives concentrations were low and comparable to those low concentrations deposited in the older sediments. But whereas during periods of low pigment deposition in the older sediments the amounts of preserved carotenoids were extremely small, the concentrations of carotenoids in all three samples from the more recent sediments (45, 35, 10 cm), declined only slightly more than the chlorophyll concentrations. Therefore the CD/TC ratios in these sediments were not as high as those in the older sediments and reached levels only slightly greater than 1.0 (Fig. 7.1.). The low pigment concentrations point to a low in-lake productivity during the times of deposition of these layers. But the concurrent decline of organic matter and water content in these sediments indicate increased mineral input, and the higher pigment ratios indicate increased allochthonous input. The higher minerogenous inflow could have been responsible for the low pigment concentrations in these sediments by diluting the autochthonously produced pigments. The autochthonous origin of the pigments is shown by the carotenoid concentrations which were not much lower than the chlorophyll derivatives concentrations. This is in contrast to the periods of low pigment deposition in the older sediments of the core in which apparently the organic matter was derived allochthonously as was indicated by the very high pigment ratios.

During all periods of either low productivity and/or increased mineral input causing high turbidity of the lake waters, all biological parameters studied (Chironomidae, Cladocera, and diatoms) responded negatively to the disturbances which was expressed especially in extremely low fossil densities in samples derived from sediments deposited during these periods. In contrast, in sediment layers in which higher pigment concentrations were preserved, fossil remains of both animal groups and the diatoms occurred with higher abundances.

After the cessation of the basal clay/silt deposition the progressive increase in the organic matter content of the sediments to the first maximum in the core, and then the abrupt decline of organic matter in the sediments above the 295 cm horizon, indicated a temporary period of relatively high lake productivity. Increasing autochthonous productivity was also suggested by an increase in pigment concentrations in these sediments. Chlorophyll derivatives reached their maximum concentration in the older sediments (326 cm to 175 cm) at the 317 cm horizon, whereas the concentration of total carotenoids peaked later in the 301 cm sample (Fig. 7.1.). The early chlorophyll derivatives' peak might have been the consequence of an early abundant development of macrophytes in the lake as was indicated by the short-termed dominance of Orthocladiinae sp. IX in the oldest organically rich sediments of the core (see Chapter V). Rapid pigment accumulation may result from the drift of littoral plant fragments to deeper sediments (Sanger & Crowl, 1979; Sanger, 1988). These littoral plant remains can contain undecomposed chlorophyll molecules in parenchymatous fragments so that the concentrations of chlorophylls could be relatively high in comparison with the carotenoids concentrations. Carotenoids derived from littoral areas would be less well preserved through a possible longer exposure time to oxidizing conditions or resuspension of deposited material, resulting in a relatively high CD/TC ratio. The pigment ratio in the 317 cm sample was greater than 1.0 indicating the possible input of organic material derived from littoral areas. If there was a terrestrial source of part of this organic material, it would have been only a small percentage because the CD/TC ratio in the 317 cm sample was relatively low in comparison with those in the samples at 321, 258 and 198 cm, in which allochthonously derived material was indicated.

According to Sanger (1988) a predominance of carotenoids, especially of the xanthophylls, over chlorophyll derivatives in the sediments can be found if a lake is largely dominated by phytoplankton (Gorham & Sanger, 1976). The maximum concentration of carotenoids in the older sediments between ca. 6000 and 3000 yr B.P. was reached in the 301 cm sample indicating a possible increase of autochthonously produced input to the sediments. The CD/TC ratio in this sample declined to one of the lowest values in the core. Sanger and Crowl (1979) presented characteristic values of pigment ratios for lakes with different trophic states. According to these authors oligotrophic lakes have CD/TC ratios of 0.5-1.0, whereas eutrophic lakes exhibit ratios between 0.3-0.5. The relatively low pigment ratio of 0.62 in the 301 cm sample would therefore indicate still oligotrophic waters during this period but at the more productive end of oligotrophy or tending towards mesotrophy.

The ratio between chlorophyll derivatives and total carotenoids, when low (<1.0) may indicate high primary production, low allochthonous input (Likens & Davies, 1975) and anaerobiosis (Sanger & Crowl, 1979; Rybak et al., 1987).

High relative abundances of Fragilaria in the sediments between 319 and 295 cm indicated a shallow lake with abundant macrophytes (see Chapter 3.8) so that it is unlikely that the peak concentration of carotenoids at the 301 cm sample was caused by a marked improvement of preservation conditions for carotenoids (e.g. anoxic conditions at the sediment-water interface) but instead might be due to an increase in autochthonous production. The increase in autochthonous production might have been caused by either phytoplankton development or increased benthic algae production. A comparison of core-wide mean pigment concentrations in cores taken from a transect across the basin of Paul Lake, Michigan, by Leavitt and Carpenter (1989) suggested that cores taken within the photic zone are influenced by benthic algal production and will not represent historical ecological dynamics in the water column.

From the 317 cm horizon upwards, the relative abundance of Corynocera increased progressively and reached the maximum level of 41.9% in the older sediments of the core (below 160 cm) in the 300 cm sample (see

Chapter V). This maximum is concurrent with the maximum of carotenoids in the 301 cm sample. As described earlier (see Chapter V), larvae of Corynocera prefer flocculent sediments with large amounts of benthic algae. The fossil diatom flora of the oldest organically rich sediments contained only a relatively low percentage of epipelic diatoms (Fig. 3.4.) but other algae could have been abundant in the benthic region of the lake. Kajak and Warda (1968) found besides diatoms mainly epipelic species of Chlorophytes and Cyanophytes in surficial profundal sediments from three lakes in Poland. The concurrent abundance maximum of Corynocera and concentration maxima of carotenoids at the 301-300 cm level might indicate that the high carotenoid deposition was caused at least in part by a high benthic algal production. A slight increase in phytoplankton productivity might have occurred simultaneously. This suggestion is supported by two reasons. In later periods, especially in the sediment layers between 225 and 220 cm, Corynocera was the dominant component of the fossil chironomid fauna occurring with a relative abundance of nearly the same level as in the 300 cm sample, but the concentration of carotenoids was lower than in the 301 cm sample. Therefore the correlation between the abundance of Corynocera and the concentration of sedimentary carotenoids derived from benthic algal populations might be not as strong as was indicated by the conditions in the 301-300 cm horizon. But it needs to be mentioned that the fossil densities in the 225-220 cm layer were considerably lower than in the oldest organically rich sediments (Table II.3.) so that it could be argued that lower densities of Corynocera remains might indicate a decline in benthic algal production and therefore a lower deposition of pigments.

Another reason suggesting that the high carotenoid concentration in the 301 cm sample was caused partially by an increase in phytoplankton growth is the abundance maximum of Daphnia during the first period of relatively high organic matter deposition in the core. In these sediments the relative abundance of Bosmina was at its minimum (Fig. 6.2.). The highest relative abundance of Daphnia in the Lake Grasmere core did not exceed 20.1% (in the 305 cm sample) of the total fossil Cladocera at any sampling level. It has been shown (Leavitt & Brown, 1988; Leavitt et al., 1989) that sedimentary pigment accumulation is influenced by the size of herbivorous grazers occurring in the zooplankton of any given lake.

Herbivore grazing in combination with photo-oxidation regulate pigment flux from the photic zone (Carpenter et al. 1986). Grazing by small-bodied zooplankton rapidly degrades pigments because their small and light faeces particles remain in the photic zone for a longer period of time. During this retention time in the photic zone the faeces particles are exposed to photo-oxidation which can completely destroy detrital pigments within a few days. Large cladocerans and copepods produce faeces particles which sink rapidly enough to bypass the photo-oxidation (Carpenter & Bergquist, 1985). Although grazing by large herbivores also reduces absolute pigment abundance, pigment concentrations per gram of organic matter may increase due to selective degradation of unpigmented material (Leavitt & Brown, 1988). Therefore, it is possible that the relatively high abundance of Daphnia between 313 and 295 cm increased the pigment deposition in these sediment layers to some degree.

Above the 295 cm level, the concentrations of organic matter in the sediments declined considerably. Pigment concentrations were also reduced signifying either reduced in-lake production or decreased pigment preservation. Pigment levels remained stable at the 290-278 cm levels and decreased to minimum concentrations in the 260 cm sample. In the sediment layers above (225-215 cm) pigment concentrations rose to pre-disturbance levels, but declined again to the lowest concentrations in the core in the sediment layer containing the Grana minora particles. Above the sandy layer, pigment concentrations increased slowly and progressively until the 165 cm horizon. In this sediment sequence (290-165 cm), which encompassed the already discussed environmental disturbances (see 3.5.3.), carotenoid concentrations always began to decline before the chlorophyll derivatives levels were reduced and increased more slowly than the chlorophyll derivatives concentrations (Fig. 7.1.) after the cessation of the disturbance. In the core stratigraphy, these disturbances left discernable layers (Fig. 3.2., 259-260 cm, 204-196 cm). The layers are well defined in the core and might point to a relatively short-term event or series of events restricted to the period during which these sediment layers were deposited. But the pigment profiles, and also the water content and loss-on-ignition profiles in the core, indicated that apparently the disturbances in the lake and/or catchment might have started earlier and that the deterioration developed gradually,

culminating in the events that led to the deposition of the dark grey layer between 260 and 259 cm and the sandy layer in the core. This was seen especially in the carotenoid profile. Carotenoid concentrations declined to considerably lower levels than the chlorophylls and increased later than the chlorophylls after the cessation of sand deposition at 196 cm. This lag caused the high CD/TC ratios in the sediment sequence indicating increasing concentrations of allochthonous material containing badly preserved carotenoids and a possible lowering of in-lake productivity through increased turbidity.

Stable and high concentrations of both pigment types were found between 165 and 60 cm, indicating a relatively high autochthonus productivity during this period. The sediments in the core of this period showed little stratigraphic variation and Corynocera had maximum abundances throughout the period, indicating a stable environment with clear lake waters and soft surface mud with high benthic algal concentrations. The benthic algae might have produced part of the high pigment concentrations. But a proportion of the deposited pigments during this period might have been derived from the water column. This is not only indicated by the increased carotenoid concentrations but also by the higher numbers of diatom frustules recorded in these sediments (Fig. 3.4.). The CD/TC ratios in these sediments were relatively stable throughout the period and remained between 0.5 and 1.0. The lowest value was recorded in the 95 cm sample (Table 7.1.) in which the pigment ratio declined to 0.59. Pigment ratios from 0.5 to 1.0 are found in oligotrophic waters (Sanger and Crowl, 1979) so that the pigment ratios found in the sediments between 165 and 65 cm might indicate that the lake waters remained in the oligotrophic to slightly mesotrophic range throughout this period.

Concentrations of both pigment types declined in the 55 cm sample raising the pigment ratio to above 1.0. Pigment concentrations remained low and the ratios high until the 35 cm horizon (Fig. 7.1.). A third period of higher lake productivity between 30-20 cm was indicated by an increase of the organic matter content to the second maximum in the core (Fig. 3.3.). Pigment concentrations also were relatively high at the 20 cm horizon but remained lower than in the sediment sequences between 317-295 cm and 165-60 cm. In the sediments between 30 and 20 cm, the high pigment concentrations might have been

caused by production of macrophytes during this period. A maximum development of macrophytes during this period was indicated by the high abundances of Orthocladiinae sp. IX fossils and a small (but maximum concentration in the core) proportion of Detritus granosus (Fig. 3.2.) found in these sediments. If the deposited pigments originated from macrophytes, they must have been derived from deeper regions in the lake because the pigment ratio in the 20 cm sample was below 1.0 indicating relatively well-preserved carotenoids.

The fourth period of higher lake productivity was found in the top sediments of the core. This increase in productivity was possibly due to increased nutrient input caused by activities of the European settlers, as was shown by the increase of Chironomus remains in the most recent sediments of the core. The pigment ratio declined to the lowest value (0.44) in the core (Table 7.1.) pointing to slightly eutrophic waters. Concentrations of chlorophyll derivatives remained at the same level as reached earlier in the 20 cm sample but the concentrations of carotenoids increased markedly in the top sample (Fig. 7.1.). This increase in the carotenoid deposition might have been caused by a higher productivity in the water column. In the most recent sediments of the core, obligate plankton species of diatoms (especially Diatoma elongata) showed a marked increase in abundance (Fig.'s 3.4. and 3.5.) pointing to a possible rise in the water level and increased planktic development.

When interpreting palaeo-productivity based upon the stratigraphy of fossil pigments, the degree in which pigment preservation is influenced by the deposition rate of the pigments has to be considered. In the sediments from Lake Grasmere, four periods occurred during which high concentrations of chlorophyll derivatives and total carotenoids per gram of organic matter were deposited. These periods were represented by 313-295 cm, 165-60 cm, 30-20 cm, and by the top sediments of the core. Because pigment concentrations are expressed per unit of organic matter, the high concentrations signify either higher productivity in the lake during these times or ameliorated pigment preservation.

According to values given by Sanger and Crowl (1979) and Bengtson and Enell (1986) carotenoid concentrations of 11-25 pigment units/gram

organic matter are indicative of mesotrophic lakes and 25-60 units/gram organic matter of eutrophic lakes, whereas 6-10 and 10-16 units/gram organic matter of chlorophyll derivatives are characteristic for mesotrophic and eutrophic lakes respectively. According to these concentrations of pigments for the different trophic states of lakes, Lake Grasmere would have been eutrophic considering the chlorophyll derivatives and mesotrophic to eutrophic considering the total carotenoid concentrations during the four periods of elevated pigment deposition.

But the level to which the trophic state of the lake would have been changed could not have been significant. This was indicated by the low concentrations of organic matter throughout the core which displayed only two maxima of organic matter content in the sediment layers between 313-295 cm and 30-20 cm. Although pigment concentrations in these sediment layers were high, amounts of both pigments were as high or higher at the top of the core and in the sediments between 165 and 60 cm. The amount of organic matter in the latter layer was only on average 2.5% higher than the organic matter content of the older sediments between 290 and 170 cm, and the organic matter content in the top sediments was comparable to those concentrations (see Appendix, Table II.I). In the older sediments of the core, from the basal sediments up to 200 cm, the organic matter of the sediments was generally lower with an average of 6-7%, so that the higher pigment concentrations in the sediment layer between 165-60 cm do point to a proportionally higher lake productivity than in the older sediments. But the high values of the fossil pigments especially in the layer 165-60 cm and the top sediments might have been also partly due to good preservation of pigments through rapid burial of the depositing detritus by the relatively high input of silt and clay material into the lake. According to Hurley and Armstrong (1991) the retention time of pigments in the surface mixed layer of sediments determines the degree of diagenesis. Preservation is enhanced when pigments are removed at a faster rate from the surface mixed layer through an increased sedimentation rate.

The sediments between 165 and 60 cm might have had a considerable amount of benthic algae and sediments with high concentrations of benthic algae have pigment profiles dominated by benthic production

(Leavitt & Carpenter, 1989). Pigments which were produced in the benthic zone could be less subject to diagenesis because they would be the pigments fastest removed from the surface mixed layer through a relatively high influx of inorganic material.

A comparison of core pigments with pigment concentrations measured in surficial sediments shows that the present day pigment accumulation has resulted in higher levels than were ever reached in the sediments of the core (Table 7.1.). Pigments accumulated to a greater degree in the sediments of the sampling station located in the northern part of the lake at a water depth of 9 m. This was possibly due to the close proximity of macrophyte beds at this sampling station. Elodea canadensis grows down to a water depth of 8 m in Lake Grasmere (Stark, 1981).

Lake Grasmere was characterized as being mesotrophic (Stout, 1972; Flint, 1975), but based on rotifer abundance and species composition Lake Grasmere is now considered to have become increasingly eutrophic in recent years (Sanoamuang and Stout, 1993). The pigment concentrations in surficial sediments from Lake Grasmere corroborate the rotifer results, or would even describe the lake as being hypertrophic. But the pigment concentrations have to be interpreted in relation to other factors. The organic matter content of the sediments at the 9 m sampling station was 10.4% of dry weight, and 11.4% at the 12 m sampling station in the southern part of the lake. This is still a relatively low concentration of organic matter in sediments and uncharacteristic of a supposedly highly eutrophic lake. As the input of mineral matter into Lake Grasmere remains high, good preservation of pigments due to relatively rapid burial would have caused partly the high pigment concentrations in the surface mud of the lake. Therefore it appears that the recent pigment accumulation in Lake Grasmere has been influenced by two processes: an increasing in-lake productivity coupled with good pigment preservation.

A discrepancy is apparent in the values of the chlorophyll derivatives to total carotenoid ratios determined in the surficial sediment samples (Table 7.1.). According to the values given by Sanger and Crowl (1979), the pigment ratios indicate oligotrophic to mesotrophic waters which is not correct. Therefore, the relatively high pigment

ratios in the surficial sediments might reflect a proportional change in the production of the individual pigments in the lake (Swain, 1985). The factors which are responsible for the proportionally high accumulation of chlorophyll derivatives in the surface muds of Lake Grasmere are not known. Possible causes could include higher chlorophyll/carotenoid ratios in living tissue or characteristics of sediment formation which favour chloropyll preservation (Likens & Moeller, 1985). Alternatively, the relatively high pigment ratios might indicate that some portion of the deposited organic matter in Lake Grasmere was derived from allochthonous sources.

To conclude there have been periods in the history of Lake Grasmere during the last 6000 years in which lake productivity was relatively high but possibly never as high as in the most recent sediments of the core or as in the present-day lake. The increase in lake productivity might have been expressed only partially in greater phytoplankton development but also through macrophyte growth and a relatively high percentage of benthic algae. During these periods high concentrations of pigments were deposited which indicates predominance of better-preserved autochthonous organic matter. The high concentrations of pigments in parts of the Lake Grasmere core were possibly due to good preservation of pigments through rapid burial caused by relatively high inputs of minerogenous matter throughout the last 6000 years. The periods of higher lake productivity were interrupted by periods of environmental disturbances during which the mineral input into the lake was increased and the organic matter was derived from mainly allochthonous sources as was shown by high ratios of chlorophyll derivatives to carotenoids.

7.5. Summary

Concentrations of fossil pigments, in the form of chlorophyll derivatives (CD), total carotenoids (TC) and the ratio of chlorophyll derivatives to carotenoids (CD/TC) exhibited frequent and distinct fluctuations during the past 6000 years of Lake Grasmere's history. Very low concentrations of both pigment types were found in sediment layers with a high mineral content, indicating low lake productivity. The high CD/TC ratios of these sediments reflected allochthonously

derived pigments. Four periods of increased lake productivity were indicated by increased pigment deposition. Two of these periods were correlated to the maxima in organic matter, whereas the period covered by the sediments between 160 and 60 cm, and the youngest sediments, had a relatively low content of organic matter. Throughout the core the organic matter content never exceeded 17% of the dry weight of the sediments. These results showed that the increase in lake productivity had not been significant but that the high concentrations of both pigment types had been due mainly to good preservation caused by rapid burial by a continuously high input of minerogenous matter.

CHAPTER VIII

CHIRONOMIDAE REMAINS FROM SURFICIAL SEDIMENT SAMPLES FROM SELECTED LAKES IN THE SOUTH ISLAND, NEW ZEALAND.

8.1. Introduction

The study of chironomid remains from surficial sediments can provide information about how recent chironomid communities are influenced by different limnological conditions (Walker & Mathewes, 1989a). This type of analysis therefore can be useful in determining the causes of the community structure of assemblages of fossil chironomids. In comparison with conventional sampling for determining chironomid assemblages in lakes, this method is more cost-efficient and has the additional advantage that the faunal composition in surficial lake sediments is more comparable to the fossil fauna in cores (Walker & Mathewes, 1989a). Analysis of surficial sediment samples across environmental gradients can reveal the influences of different factors, such as water chemistry, climate, or lake morphology. According to Walker et al. (1984), a single surficial sample taken near a lake's maximum depth may give an adequate assessment of the fauna of a relatively small lake. Several samples should be taken in large lakes. These samples reflect the conditions of the part of the lake where the sample was collected more than the conditions prevailing in the entire lake.

8.2. Methods

A survey of the benthic chironomid fauna of 32 lakes in the South Island of New Zealand (Fig. 8.1.) was conducted during 1990 and 1991. The sediment samples were collected from each site with an Ekman grab from a small boat. Whenever possible, collections were made near the centre of the lakes or the bays of the larger lakes. After retrieval of the mud sample, the overlaying water in the Ekman grab was carefully decanted and about 50 ml of sediment, within the top 10 cm of the grab-sample, were retained. The analysis of the sediment was undertaken as described by Hofmann (1971, see Chapter II) and at least

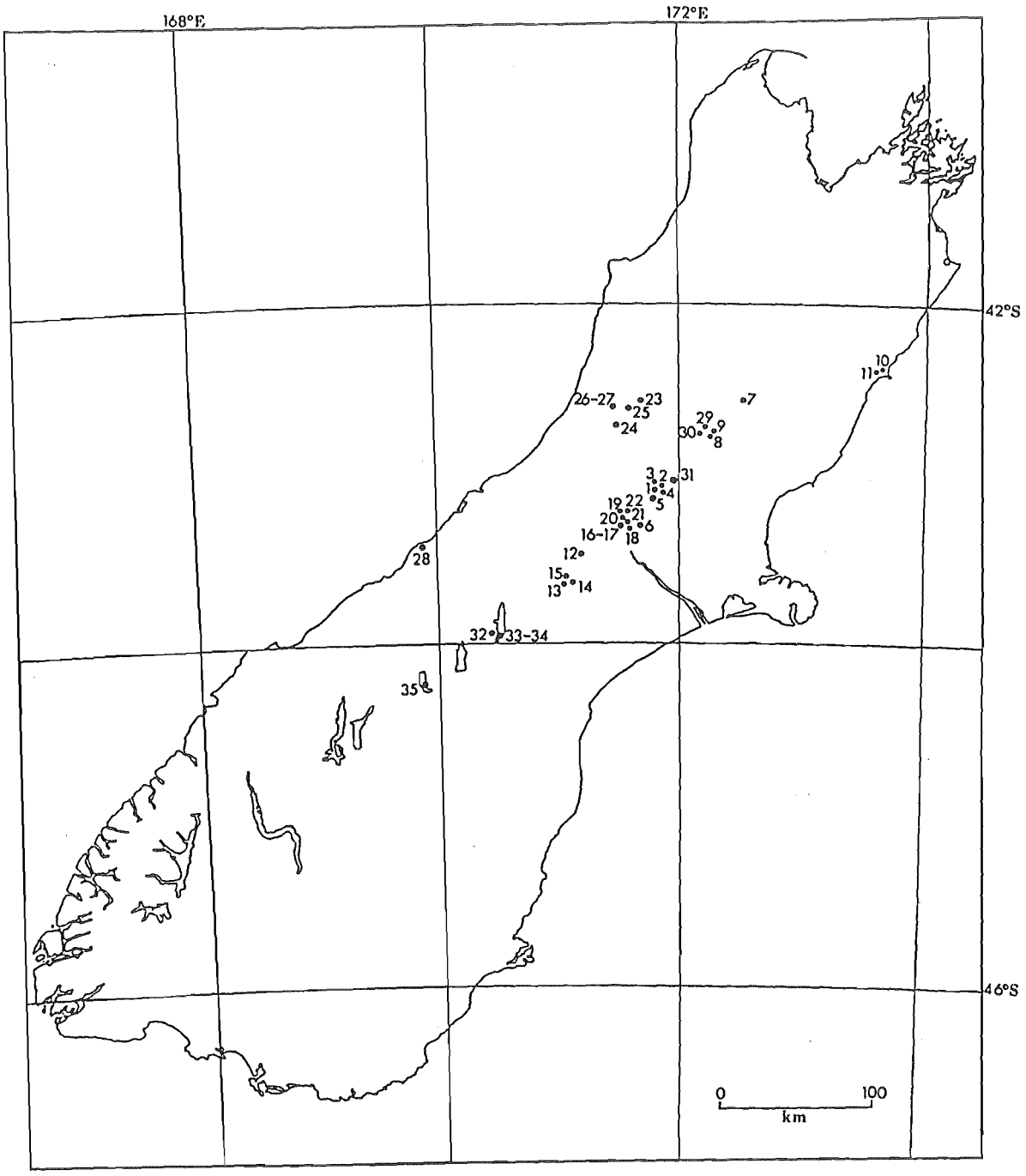


Fig. 8.1. Map of the South Island of New Zealand with indications of the locations of lakes included in the analysis of chironomid remains from surficial sediments (site code in Fig. 8.2.).

50 head capsules were retrieved per sample. For most lakes, the concentration of head capsules was sufficiently high so that it was only necessary to analyse 1-5 ml of wet sediment. But for the samples obtained from some of the large unproductive lakes in the south (Lakes Coleridge, Tekapo and Ohau, and Lake Brunner (West Coast)) which all have high mineral contents in their sediments, larger aliquots (of up to 50 ml) had to be analysed.

8.3. Study Sites

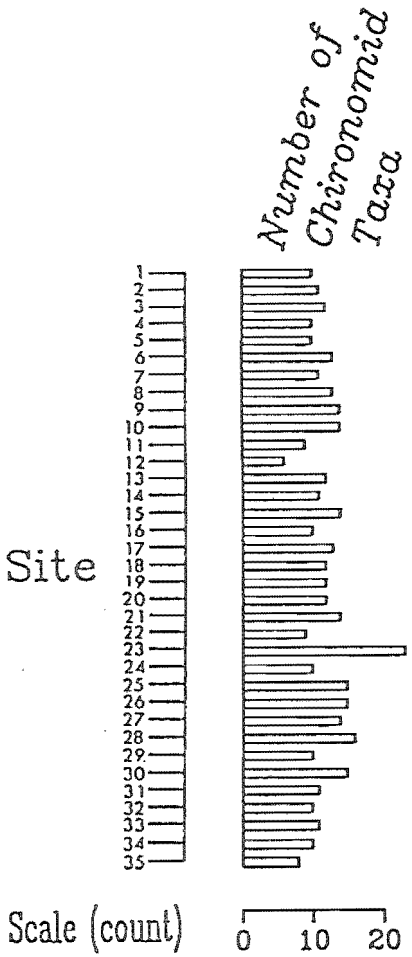
The lakes under study have been selected according to trophic state, morphology, geographical situation and accessibility. The locations and altitudes of the lakes sampled are given in Table 8.1.

Most of the lakes studied are high country lakes located to the east of the Main Divide (Fig. 8.1., Fig. 8.2. for the number code of the lakes) and at altitudes of 450 to 841 m. a.s.l. (Table 8.1.). The lowland lakes include five West Coast lakes (Brunner, Poerua, Haupiri, Matheson, and Lady Lake) and two small coastal lakes near Kaikoura (Rotorua and Rotoiti). Many of the lakes were formed at least partly by glacial action. The two lakes near Kaikoura are of recent origin formed from previous tributaries of the Kahutara and Kowhai Rivers (Stout, 1985). The catchments of many of the high country lakes are open tussock grasslands (Stout, 1969; Ward & Talbot, 1984; Livingston et al., 1986; Shanks et al., 1990). Lakes Taylor, Sheppard, Katrine, and Mason are surrounded by tussock grassland and native beech forest (De Winton et al., 1991), and the West Coast lakes are bordered by Nothofagus stands, except for Lake Brunner which is surrounded by podocarp forest. The waters of the beech forest lakes are amber-coloured. The colouring of the lake waters is a major difference with the other lakes studied (Paerl et al., 1979). The catchments of the Kaikoura lakes consists of grass-covered hills with manuka (Leptospermum sp.) and wild briar (Rubus sp.) as the dominant shrubs (Stout, 1985).

Table 8.1. Location and altitude of South Island lakes included in the study of chironomid remains from surficial sediments.

Lake	Altitude m a.s.l.	Longitude E	Latitude S	District
L. Grasmere	583	171°46.5′	43°04′	Malvern
L. Pearson	607	171°47′	43°06′	Malvern
L. Hawdon	580	171°51′	43°06.5′	Malvern
L. Marymere	616	171°51.4′	43°07.1′	Malvern
L. Sarah	560	171°46.6′	43°03′	Malvern
L. Letitia	589	171°57′	43°03.5′	Malvern
L. Lyndon	841	171°42′	43°18.3′	Malvern
Horseshoe L.	450	172°31.3′	42°35.9′	Hurunui
L. Taylor	534-609	172°14′	42°46′	Malvern
L. Sheppard	534-609	172°15′	42°46′	Malvern
L. Katrine	518-549	172°12′	42°43′	Hurunui
L. Mason	617-700	172°10.3′	42°44′	Hurunui
L. Rotoiti	40	173°35.8′	42°24.1′	Kaikoura
L. Rotorua	30	173°35′	42°24.5′	Kaikoura
L. Heron	694	171°10′	43°29′	Ashburton
L. Camp	671-701	171°03′	43°37′	Ashburton
L. Emma	657	171°03′	43°38′	Ashburton
L. Clearwater	668	171°03′	43°36′	Ashburton
L. Coleridge	507	171°30′	43°18′	Malvern
L. Georgina	545	171°34.2′	43°19.2′	Malvern
L. Selfe	579-610	171°31′	43°14′	Malvern
L. Evelyn	579-610	171°32′	43°15′	Malvern
L. Catherine	700-731	171°34′	43°13′	Malvern
L. Ida	671-700	171°32′	43°53′	Malvern
L. Alexandrina	732-763	170°27′	43°56′	Mackenzie
L. Tekapo	708	170°32′	43°53′	Mackenzie
L. Ohau	517	169°51′	44°14′	Waitaki
L. Brunner	86	171°27′	42°37′	Grey
L. Poerua	124	171°30′	42°42′	Grey
Lady Lake	91-122	171°34.5′	42°36′	Grey
L. Haupiri	152-183	171°41′	42°34′	Grey
L. Matheson	approx. 30	169°58′	43°26′	Westland

Districts according to Livingston et al. (1986).



SITE CODE

1 - L. Grasmere	13 - L. Camp	25 - Lady L.
2 - L. Hawdon	14 - L. Emma	26 - L. Brunner I
3 - L. Sarah	15 - L. Clearwater	27 - L. Brunner II
4 - L. Marymere	16 - L. Coleridge I	28 - L. Matheson
5 - L. Pearson	17 - L. Coleridge II	29 - L. Katrine
6 - L. Lyndon	18 - L. Georgina	30 - L. Mason
7 - Horseshoe L.	19 - L. Selfe	31 - L. Letitia
8 - L. Taylor	20 - L. Evelyn	32 - L. Alexandrina
9 - L. Sheppard	21 - L. Catherine	33 - L. Tekapo I
10 - L. Rotoiti	22 - L. Ida	34 - L. Tekapo II
11 - L. Rotorua	23 - L. Haupiri	35 - L. Ohau
12 - L. Heron	24 - L. Poerua	

Fig. 8.2. South Island lakes: Number of chironomid taxa in surficial sediment samples and site codes for the lakes studied.

Some limnological parameters of the lakes are summarized in Table 8.2. (lake area, maximum depth, summer temperature, and loss-on-ignition of the sediment samples studied), Table 8.3. (depth of sample, Secchi disc readings, surface temperature - all measurements were undertaken at the time of sampling of the sediment samples), and Table 8.4. (pH and chlorophyll in surface waters). The locations of the two sample stations in Lakes Coleridge, Tekapo, and Brunner are given in Table 8.3.

Most of the lakes studied are small (<2.00 km^2) and Lakes Rotoiti and Matheson have the smallest lake areas (0.03 km^2). The largest lakes are Lakes Coleridge, Brunner, Ohau, and Tekapo, and Lakes Heron and Alexandrina also have an area of >5.00 km^2. The largest lakes are also the deepest, with water depths ranging from 109.0 m (Lake Brunner) to 200.0 m (Lake Coleridge). The sampling depths of the surficial sediment samples did not exceed 45 m (in Lake Brunner I, Moana Bay), and in the other deep lakes the sampling depths ranged from 18 - 25 m (Table 8.3.). The shallower lakes were sampled, if possible, near to the centre so that the sampling depths are closer to the maximum depths of these lakes. In Lake Heron, sampling was only possible nearer to the shore due to adverse weather conditions on the sampling day.

The highest measured summer temperatures (Table 8.2.) for most lakes were in the range between 17° and 21°C. Some of the larger lakes furthest south had lower summer temperatures. These included Lakes Coleridge (15.0°C), Tekapo and Ohau (14.5°C). Lake Poerua had a slightly higher summer temperature of 23°C and the two coastal lakes near Kaikoura had the highest summer temperatures of 27°C. The Secchi disc readings ranged from very low values in the two Kaikoura lakes (0.2 m) to the extremely clear waters of Lake Letitia (11 m) (Table 8.3.). Loss-on-ignition was measured for all surficial sediment samples included in the study (Table 8.2.). The organic matter content in the sediments of the large lakes was very low, especially in Lakes Tekapo, Brunner and Ohau. The lowest value of 2.5% of dry weight was measured in Lake Tekapo I. The organic matter content in the sediments of most of the other lakes ranged from 9% to 29% (Lake Marymere). The maximum value of 62% was measured in Lake Evelyn. The pH of the waters (Table 8.4.) in most lakes ranged from only slightly acidic to

Table 8.2. Some characteristics of South Island lakes from which surficial sediments were analysed for chironomid remains (L-o-I: Loss-on-ignition).

Lake	Lake Area (km^2)	Max. Depth (m)	Summer Temp. (°C)	L-o-I (*)
L. Grasmere	0.67	15.0	19.0	11.1
L. Pearson	1.79	17.0	17.0	11.1
L. Hawdon	0.30	4.0	18.2	27.9
L. Marymere	0.23	7.0	18.9	29.3
L. Sarah	0.20	7.0	21.0	23.0
L. Letitia	0.28	18.0	19.4	19.7
L. Lyndon	1.11	28.0	18.0	9.5
Horseshoe L.	0.35	10.0	19.2	17.1
L. Taylor	1.85	40.5	15.5	9.2
L. Sheppard	1.15	21.0	15.5	15.7
L. Katrine	0.75	28.0	15.1	7.1
L. Mason	1.00	38.5	13.8	11.4
L. Rotoiti	0.03	1.5	27.0	22.3
L. Rotorua	0.55	3.0	27.0	18.2
L. Heron	6.30	37.0	18.8	12.7
L. Camp	0.49	18.0	20.6	14.5
L. Emma	1.55	3.0	21.3	21.6
L. Clearwater	1.98	18.0	21.2	9.2
L. Coleridge	32.9	200.0	15.0	8.5 (I) 9.5 (II)
L. Georgina	0.20	10.0	17.6	10.6
L. Selfe	0.33	30.0	19.8	9.7
L. Evelyn	0.15	3.0	18.9	62.6
L. Catherine	0.15	4.9	12.0	5.8
L. Ida	0.10	9.0	17.8	5.1
L. Alexandrina	5.80	30.0	17.0	17.8
L. Tekapo	86.8	120.0	14.5	2.5 (I) 3.6 (II)
L. Ohau	53.85	129.0	14.5	3.7
L. Brunner	36.1	109.0	17.8	6.2 (I) 2.3 (II)
L. Poerua	2.15	7.8.0	23.0	14.7
Lady Lake	1.25	23.0	18.0	21.6
L. Haupiri	2.1	20.0	17.5	11.6
L. Matheson	0.3	12.0	20.6	27.1

Lake data from Livingston et al. (1986), Stout (1985) (L. Rotoiti and Rotorua), Temperatures for Lakes Katrine, Mason, and Matheson (Stout, pers. comm.), Temperatures for Lakes Horseshoe, Taylor, Sheppard, Heron, Camp, Emma, Alexandrina, Tekapo, and Ohau (pers. obs.).
(*) Loss-on-ignition as percent of dry-weight.

Table 8.3. Some parameters of South Island lakes at time of sampling of surficial sediments.

Lake	Depth of sample (m)	Secchi D. (m)	Surface Temp.(°C)	Sampling Date
L. Grasmere	12.0	1.9	15.8	18/1/90
L. Pearson	13.0	3.3	17.0	17/1/90
L. Hawdon	2.5	2.5	16.0	17/1/90
L. Marymere	5.5	5.2	16.0	17/1/90
L. Lyndon	21.0	5.0	17.0	18/1/90
L. Sarah	5.0	2.8	15.5	17/1/90
L. Letitia	15.0	11.2	14.2	25/10/90
Horseshoe L.	9.0	0.9	19.2	22/1/90
L. Taylor	36.0	4.1	15.5	21/1/90
L. Sheppard	10.0	3.5	15.5	21/1/90
L. Katrine	25.0	3.7	15.1	9/3/76*
L. Mason	30.0	6.6	13.8	10/3/76*
L. Rotoiti	0.6	0.2	23.0	16/2/90
L. Rotorua	2.0	0.3	23.0	16/2/90
L. Heron	4.0	3.8	18.8	23/2/90
L. Camp	17.0	5.1	20.6	22/2/90
L. Emma	2.1	1.6	21.3	22/2/90
L. Clearwater	17.0	3.0	21.0	22/2/90
L. Coleridge I	18.0	7.0	11.4	31/5/90
L. Coleridge II	25.0	5.5	11.0	31/5/90
L. Georgina	8.3	8.3	7.0	31/5/90
L. Selfe	22.0	5.3	8.2	31/5/90
L. Evelyn	3.0	3.0	6.0	27/6/90
L. Catherine	1.5	1.3	7.5	27/6/90
L. Ida	9.0	5.0	3.8	27/6/90
L. Alexandrina	25.0	4.4	17.0	16/1/91
L. Tekapo I	24.0	1.1	14.5	16/1/91
L. Tekapo II	25.0	1.0	14.4	16/1/91
L. Ohau	25.0	1.3	14.5	17/1/91
L. Brunner I	45.0	5.8	10.2	25/7/90
L. Brunner II	23.0	6.3	10.2	25/7/90
L. Poerua	6.0	3.2	10.1	24/7/90
Lady Lake	20.0	1.5	8.6	25/7/90
L. Haupiri	18.0	1.3	7.7	26/7/90
L. Matheson	11.0	1.5	-	31/1/78*

* Samples taken by Dr. V.M. Stout.
Sample stations in
Lake Coleridge: I-South-east Basin, II- Ryton River Bay;
Lake Brunner: I-Moana Bay, II-Iveagh Bay;
Lake Tekapo: I-offshore from Mt. John, II-opposite
Tekapo I, sampling station on eastern side of the lake.

Table 8.4. South Island Lakes: Measurements of some environmental variables at time of sampling.

Lake	ph	Chlorophyll mg/m^3	Sampling Date
L. Grasmere	7.90	12.653	18/1/90
L. Pearson	7.05	2.354	17/1/90
L. Hawdon	6.95	0.485	17/1/90
L. Marymere	7.05	0.919	17/1/90
L. Lyndon	7.00	0.934	18/1/90
L. Sarah	7.00	3.836	17/1/90
L. Letitia	6.90	0.321	25/10/90
Horseshoe L.	7.1	25.160	23/1/90
L. Taylor	7.15	2.172	24/1/90
L. Sheppard	7.15	5.476	23/1/90
L. Katrine	7.4	1.508	9/3/76
L. Mason	7.5	1.179	10/3/76
L. Rotoiti	6.9	327.292	16/2/90
L. Rotorua	7.3	12.749	16/2/90
L. Heron	6.95	0.706	23/2/90
L. Camp	6.95	1.269	21/2/90
L. Emma	7.35	3.776	22/2/90
L. Clearwater	7.0	4.349	22/2/90
L. Coleridge I	6.9	0.823	31/5/90
L. Coleridge II	6.9	0.277	31/5/90
L. Georgina	6.85	0.591	31/5/90
L. Selfe	6.8	2.189	31/5/90
L. Evelyn	6.95	1.176	27/6/90
L. Catherine	6.95	0.842	27/6/90
L. Ida	7.0	2.291	27/6/90
L. Alexandrina	7.3	4.876	16/1/91
L. Tekapo I	7.2	0.367	16/1/91
L. Ohau	7.1	0.983	17/1/91
L. Brunner I	6.8	0.730	25/7/90
L. Brunner II	6.8	0.679	25/7/90
L. Poerua	6.7	2.865	24/7/90
Lady Lake	6.7	0.883	25/7/90
L. Haupiri	6.8	0.564	26/7/90
L. Matheson	5.1	7.172	31/1/78

All data in this table courtesy of Dr. V.M. Stout, Zoology Department, University of Canterbury, (unpublished).

slightly alkaline. The only exception was Lake Matheson, with a pH of 5.1 (Table 8.4.). The chlorophyll concentrations in most lakes were relatively low (Table 8.4.). Highest values were measured in Lakes Rotorua, Grasmere and Horseshoe Lake, and an unusually high value of 327.292 mg/m^{-3} was recorded for Lake Rotoiti.

These data show that the range of the limnological parameters in the lakes studied exhibited a wide range of conditions, to which it might be possible to relate the composition of the fossil chironomid fauna in the surficial sediment samples.

8.4. Results

In the surficial sediment samples from the 32 lakes studied, head capsules of six chironomid subgroups were found (Fig. 8.3.). Heptagyini and Podonominae were rare. Heptagyini occurred only in seven lakes and were most abundant in Lake Coleridge II and Lady Lake. Podonominae were found in six lakes but were most common in Lake Coleridge II.

The abundances of the remaining four subgroups, Chironomini, Orthocladiinae, Tanypodinae, and Tanytarsini, varied greatly in the different lakes. Chironomini were found in relatively high abundances in all lakes except for Lakes Poerua, Evelyn, Catherine and Marymere, in which the relative abundance of Chironomini was lower than 10%. The lakes which had a relative abundance of Chironomini of more than 50% included Lakes Pearson, Lyndon, Rotoiti, Rotorua, Heron, and Alexandrina. In all lakes with a low occurrence of Chironomini, Orthocladiinae were the major group with abundances over 50% of the total fauna. In Lake Marymere, 84.1% of the chironomid head capsules belonged to the Orthocladiinae, the highest percentage found in the samples. Other lakes with a high proportion of Orthocladiinae were Horseshoe (50.0%), Georgina (54.0%), Evelyn (67%), Catherine (50.0%), Poerua (78.9%), Brunner I (72.9%), Brunner II (73.5%), Tekapo I (50.8%) and Lady Lake (55.8%). A relative abundance of less than 10% of this subfamily was recorded only in Lake Rotoiti near Kaikoura and Loch Katrine. The abundances of Tanytarsini and Tanypodinae were generally lower than those of Chironomini and

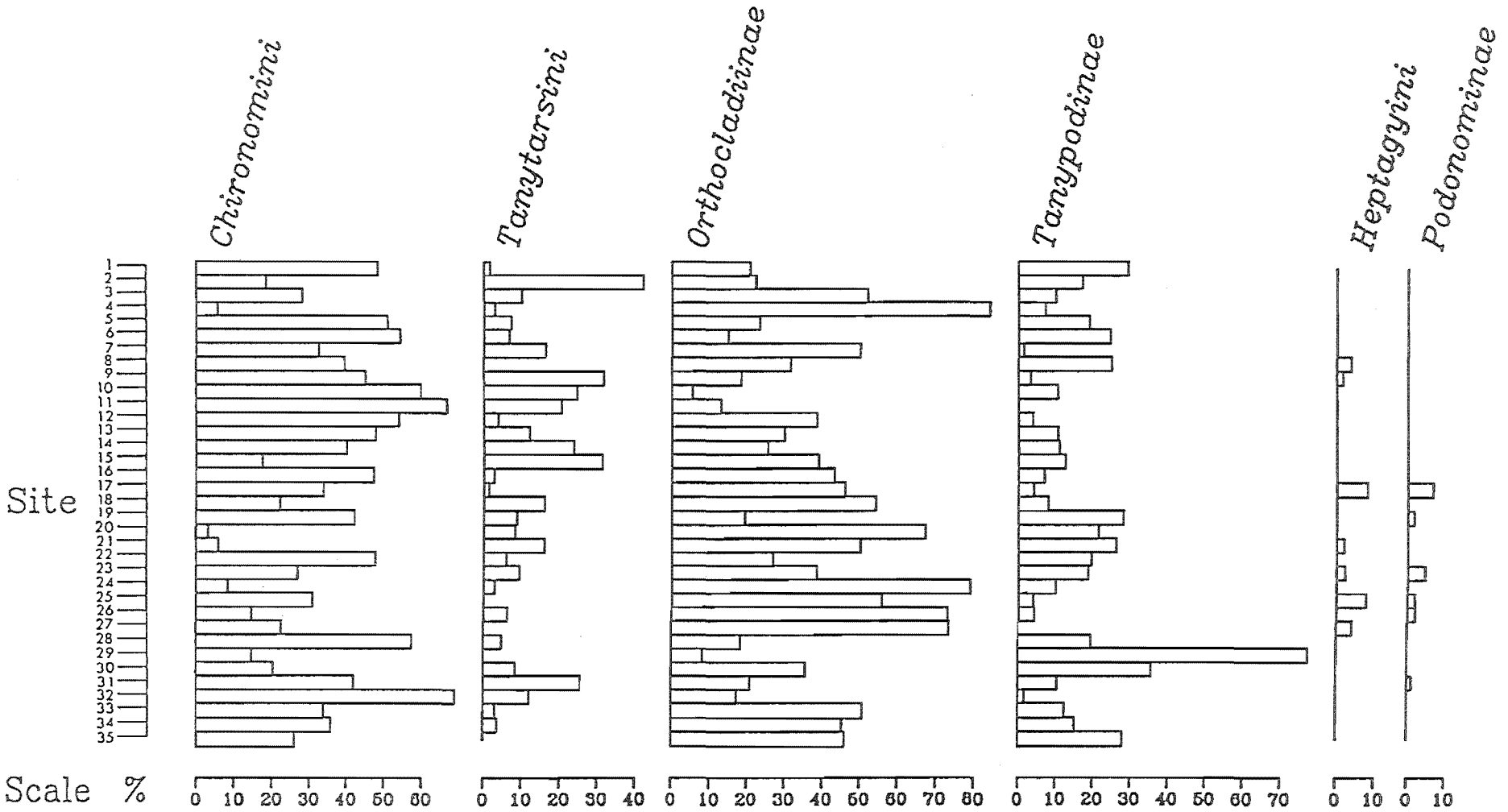


Fig. 8.3. South Island lakes: Relative abundance (as percent of the total number of chironomid remains in the samples) of the chironomid subgroups in the surficial sediment samples.

Orthocladiinae. Only the chironomid fauna of Lake Hawdon was dominated by Tanytarsini (42.1%), while in the samples from Lakes Sheppard and Clearwater, Tanytarsini abundances of more than 30% were found. The samples of Lakes Taylor, Katrine, Brunner (Iveagh Bay), and Lady Lake did not contain any Tanytarsini head capsules. Tanypodinae were present in most lakes, except for Lake Heron and the Iveagh Bay of Lake Brunner (II), and occurred only in Lakes Grasmere, Sheppard and Clearwater with a relative abundance higher than 30%.

A total of 37 chironomid taxa could be distinguished in the surficial sediment samples (Table 8.5.). In most lakes, the number of chironomid taxa varied between 10 and 15. Only six taxa were found in Lake Heron, in Lake Ohau eight chironomid taxa, and in Lakes Ida and Rotorua nine chironomid taxa. A higher taxa number than 15 occurred in only two lakes: 16 taxa were found in Lake Matheson, and dystrophic Lake Haupiri showed the maximum number of 23 chironomid taxa (Fig.8.2.). Orthocladiinae (13 taxa) and Chironomini (10 taxa) were the most diverse chironomid subgroups, followed by the Tanypodinae (6 taxa), Tanytarsini (4 taxa), Heptagyiini (possibly 3 taxa) and Podonominae with only two taxa. The highest number of as yet undescribed species was found in the Orthocladiinae.

Table 8.5. Chironomidae taxa found in surficial sediment samples from South Island lakes.

Chironomini

Chironomus spp.
Paucispinigera sp.a
Polypedilum spp.
Riethia
Cladopelma curtivalva (Kieffer, 1917)
Chironomini sp. A
Parachironomus cylindricus (Freemann, 1959)
Cryptochironomus
Xenochironomus canterburyensis (Freemann, 1959)
Kiefferulus opalensis (Forsyth, 1975)

Tanytarsini

Corynocera
Tanytarsus vespertinus (Hutton, 1902)
Tanytarsus funebris (Freeman, 1959)
Paratanytarsus

Orthocladiinae

Orthocladiinae sp. IX
Cricotopus spp.
Cricotopus (?) *aucklandensis (Sublette & Wirth, 1980)*
Corynoneura
Orthocladiinae XIV
Orthocladiinae VIII
Eukiefferiella
Eukiefferiella claripennis gr.
Orthocladiinae XV
Matakiri
Orthocladiinae sp. V
nr. *Synorthocladius*
Orthocladiinae sp. XIII

Tanypodinae

Apsectrotanypus
Tanypodinae sp. I
Macropelopia
nr. *Pentaneura*
Gressittius antarcticus (Hudson, 1892)
Tanypodinae sp. II

Heptagyini

Maoridiamesa
Heptagyini spp.

Podonominae

Parochlus
Podonomus

The distribution of the most abundant Chironomidae taxa in surficial sediment samples from South Island lakes is given in Fig. 8.4. Chironomus head capsules were the most numerous. The chironomid fauna of 14 lakes was dominated by Chironomus (with a relative abundance of >30%). These lakes included Grasmere, Pearson, and Lyndon of the Cass lakes, Lakes Heron, Camp and Emma, Lakes Taylor and Sheppard, Lake Rotorua, Horseshoe Lake, Lakes Selfe and Ida in the vicinity of Lake Coleridge, also both sampling stations in Lake Coleridge, and Lake Alexandrina. Further common Chironomini taxa were Polypedilum, Cladopelma, Paucispinigera sp. a and Chironomini A. Chironomini A occurred in relatively low abundances in most lakes studied. Paucispinigera sp. a was dominant in Lake Matheson (45.1%), abundant in Lake Tekapo II (28.0%) and common in Lake Tekapo I (10.8%). Cladopelma was dominant in Lake Rotoiti (40.3%), occurred in Lake Letitia with a relative abundance of 11.4%, but was rare in most of the other lakes studied. Polypedilum was common in Lake Hawdon (11.8%) but occurred only in a small number of lakes and in low abundances. Kiefferulus was only found in Lakes Rotoiti (5.3%) and Rotorua (12.9%). The rare Chironomini taxa, Parachironomus, Xenochironomus, and Cryptochironomus, were found mostly as single head capsules in a small number of lakes (see Appendix, Table III.2.).

Orthocladiinae sp. IX was the dominant orthoclad and was the most abundant form in the fauna of eleven sites including Lakes Sarah, Marymere, Clearwater, Georgina, Evelyn, Poerua, Brunner I and II, Tekapo I and II, and Ohau. In Lakes Heron and Coleridge I, this taxon was sub-dominant. The highest relative abundance of one single taxon was found in Lake Marymere, where 81.2% of all head capsules found belonged to Orthocladiinae sp. IX. In most cases, the lakes with high abundances of Orthocladiinae sp. IX had low abundances of Chironomus. Cricotopus sp. was found in nearly every lake and had abundances of 15% or higher in Lakes Grasmere, Sarah, Poerua, Brunner I, and Tekapo I and II. Cricotopus aucklandensis was the dominant chironomid in Horseshoe Lake (29.4%) but generally occurred with a relative abundance of <10%. Eukiefferiella was abundant in two lakes, Lady Lake (23.0%) and Lake Brunner II (20.4%), and was also found in Lakes Brunner I, Ohau, and the four lakes located in the upper catchment of the Hurunui River, Lakes Taylor, Sheppard, Katrine and Mason. Eukiefferiella claripennis, Orthocladiinae sp. VIII (possibly

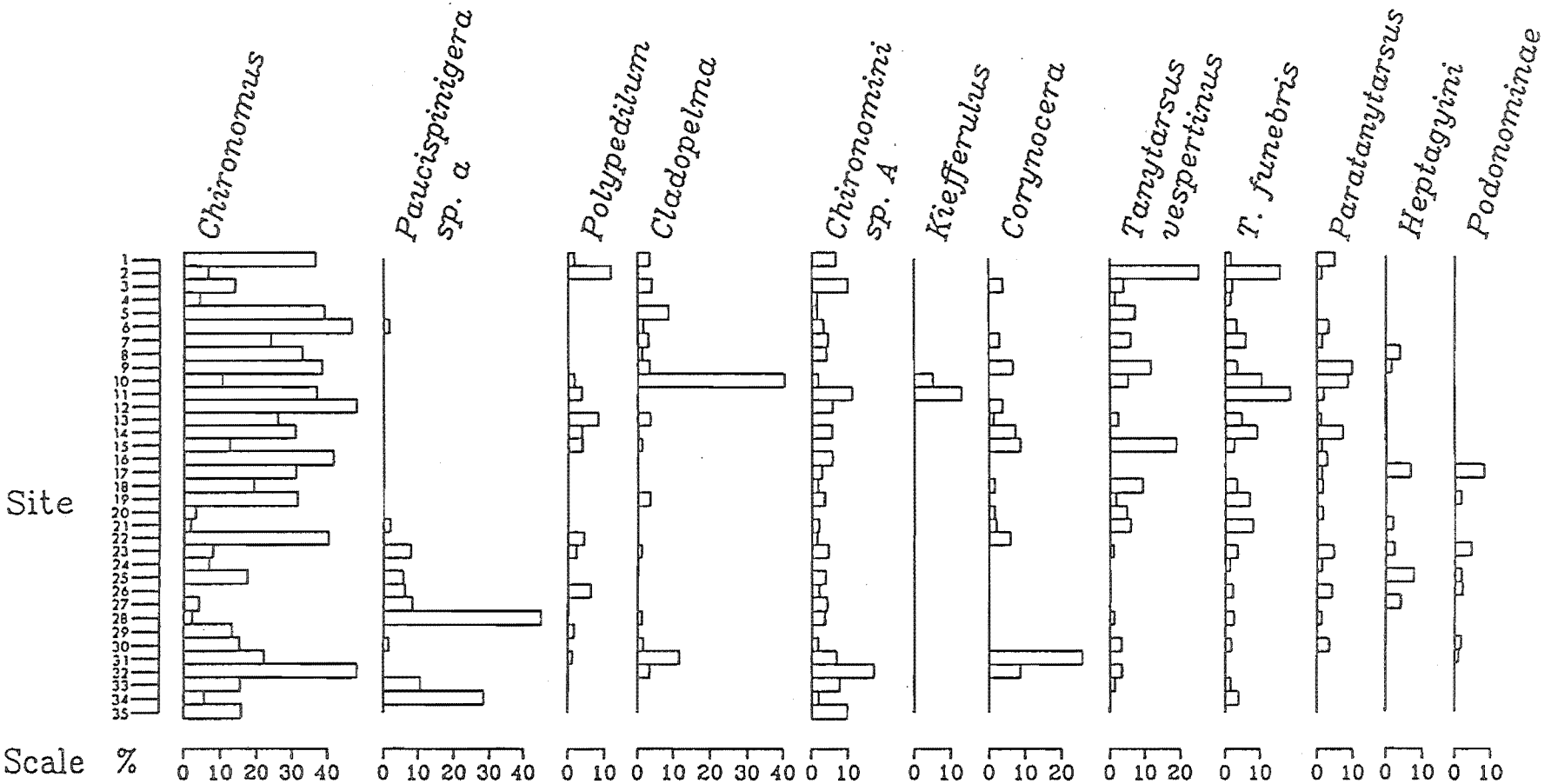


Fig. 8.4. Part 1: South Island lakes: Percentage diagram (as percent of the fossil sum in the samples) of selected chironomid taxa in the surficial sediment samples.

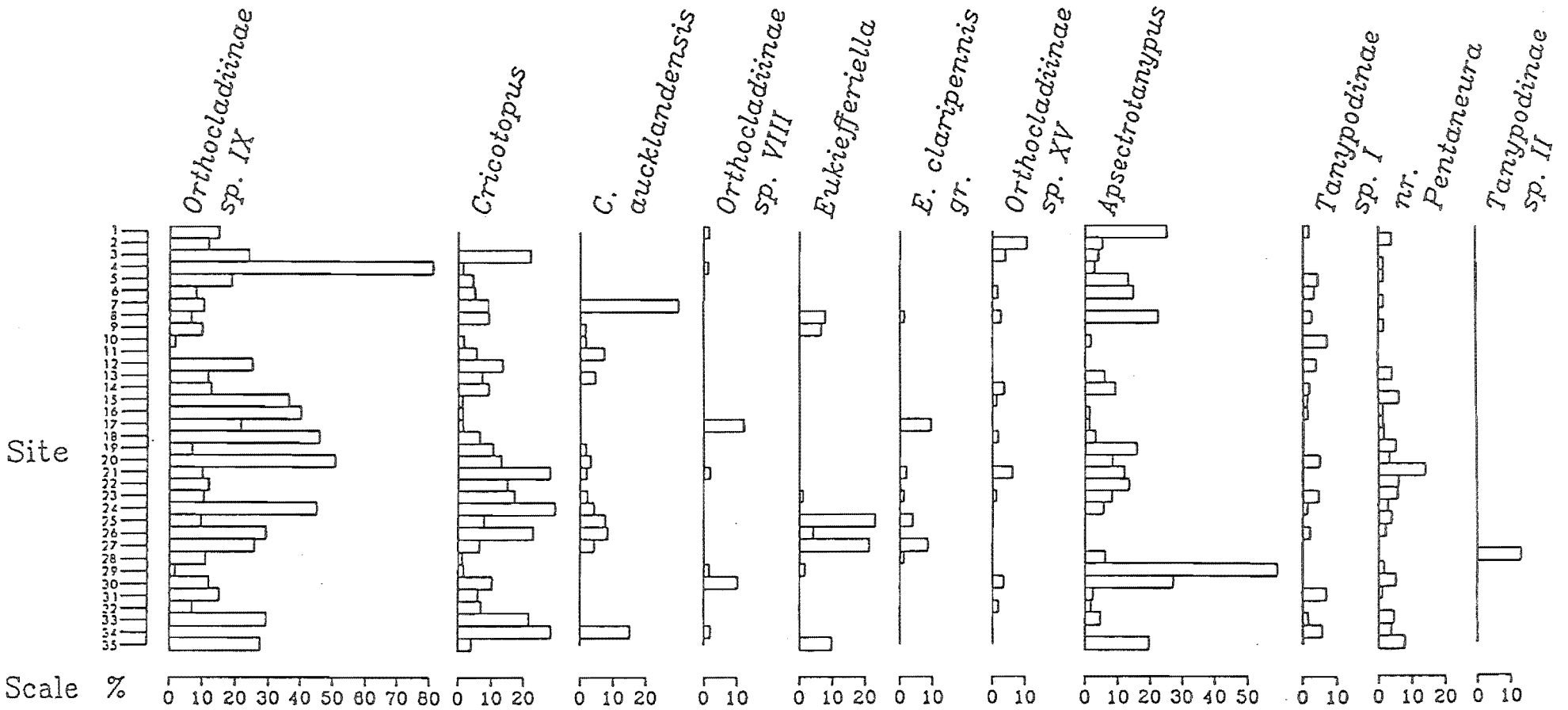


Fig. 8.4. Part 2: South Island lakes: Percentage diagram (as percent of the fossil sum in the samples) of selected chironomid taxa in the surficial sediment samples.

Naocladius, see Chapter IV), and Orthocladiinae sp. XV occurred in small abundances in only a small number of lakes. The remaining six Orthocladiinae taxa were rare. These included Corynoneura, Orthocladiinae XIV, Matakiri, Orthocladiinae sp. V, nr. Synorthocladius and Orthocladiinae sp. XIII. Only three head capsules of Orthocladiinae XIII have been found, all of them in Lake Ohau (see Appendix, Table III.2.).

In the Tanytarsini, head capsules belonging to Tanytarsus vespertinus occurred with the highest abundance. This species was the dominant form of the fauna of Lake Hawdon (25.0%). T. funebris was found in most surficial sediment samples but was most abundant in Lakes Hawdon (15.8%) and Rotorua (18.5%) and was common in Lake Rotoiti (10.5%). Corynocera occurred with its highest abundance in Lake Letitia (25.6%), where it was the dominant chironomid in the fauna. In most lakes studied this taxon was not present or rare with the exception of Lakes Alexandrina (8.6%), Clearwater (8.8%) and Emma (7.3%). Paratanytarsus was found in many of the lakes studied but only in low numbers.

Of the five Tanypodinae taxa found, only Apsectrotanypus was relatively abundant in most of the lakes studied. This taxon dominated the fauna of Loch Katrine (59% relative abundance) and was abundant (>20%) in Lakes Grasmere, Taylor, Mason, and Ohau. Nr. Pentaneura was found in most lakes but was only abundant in Lake Catherine (14.0%). The undescribed Tanypodinae sp. I occurred in low numbers in many of the lakes studied, whereas Tanypodinae sp. II was found only in Lake Matheson, where it occurred with a relative abundance of 13.4%. Head capsules of Gressittius were rare with the exception of Loch Katrine, where this taxon accounted for 11.5% of the fauna, and those of Macropelopia were slightly more abundant (see Appendix, Table III.2.). Macropelopia was most common in Lakes Selfe (7.0%) and Katrine (4.9%).

In summary, although a total of 37 chironomid taxa have been found in the surficial sediments of the 32 lakes studied, it has been shown that the fauna in most lakes was dominated by only a relatively small number of taxa. The dominant taxa were Chironomus, Orthocladiinae sp. IX, Cricotopus sp. and Apsectrotanypus.

8.4.1. Numerical Analyses

For the numerical analyses, a classification and correspondence analysis (see Chapter II), the data matrix consisted of the percentage abundance of 19 species in 35 surficial sediment samples (for the taxa in question see Table 8.6.). Taxa that did not constitute >2% of the fauna were excluded, but the original percentage calculations derived from the entire fauna were kept for the 19 taxa included in the numerical analyses. The hierachical classification analysis was based on the percentage similarity of community (PSc-index). The dendrogram of the group average clustering is presented in Fig. 8.5. Three groups of surficial sediment samples were formed, and four lakes were classified as outliers. The outliers were Loch Katrine which differed the most from all the other lakes studied, and Lakes Hawdon, Rotoiti, and Matheson.

The following groups of lakes were formed (the numbers in brackets are the site code numbers, which are also used in the ordination diagram):
Group I: Lakes Mason (30), Ohau (35), Catherine (21), Brunner I (26), Sarah (3), Tekapo I (33), Haupiri (23), and Tekapo II (34).
Group II: Lakes Marymere (4), Clearwater (15), Georgina (18), Evelyn (20), and Poerua (24).
Lady Lake (25) and Lake Brunner II (27) are a sub-group to groups I and II.
Group III: Lakes Letitia (31), Horseshoe (7), Sheppard (9), Rotorua (11), Alexandrina (32), Coleridge II (17), Heron (12), Coleridge I (16); and sub-group IIIa which contains the closest grouped lakes in this group: Lakes Camp (13), Emma (14), Ida (22), Selfe (19), Grasmere (1), Taylor (8), Pearson (5), and Lyndon (6).

The chironomid fauna of lakes belonging to Group I (Table 8.6.) was characterized by very low abundances of Chironomus, relatively high abundances of Orthocladiinae sp. IX and the maximum abundance of Cricotopus sp. The abundances of Tanytarsini were low, and in the Tanypodinae Apsectrotanypus and nr. Pentaneura occurred with their highest abundances. Also Paucispinigera sp. a had its maximum relative abundance in this sample group. Lakes belonging to Group II had a chironomid fauna in which Orthocladiinae sp. IX was by far the dominant chironomid. Amongst the Orthocladiinae Cricotopus was the

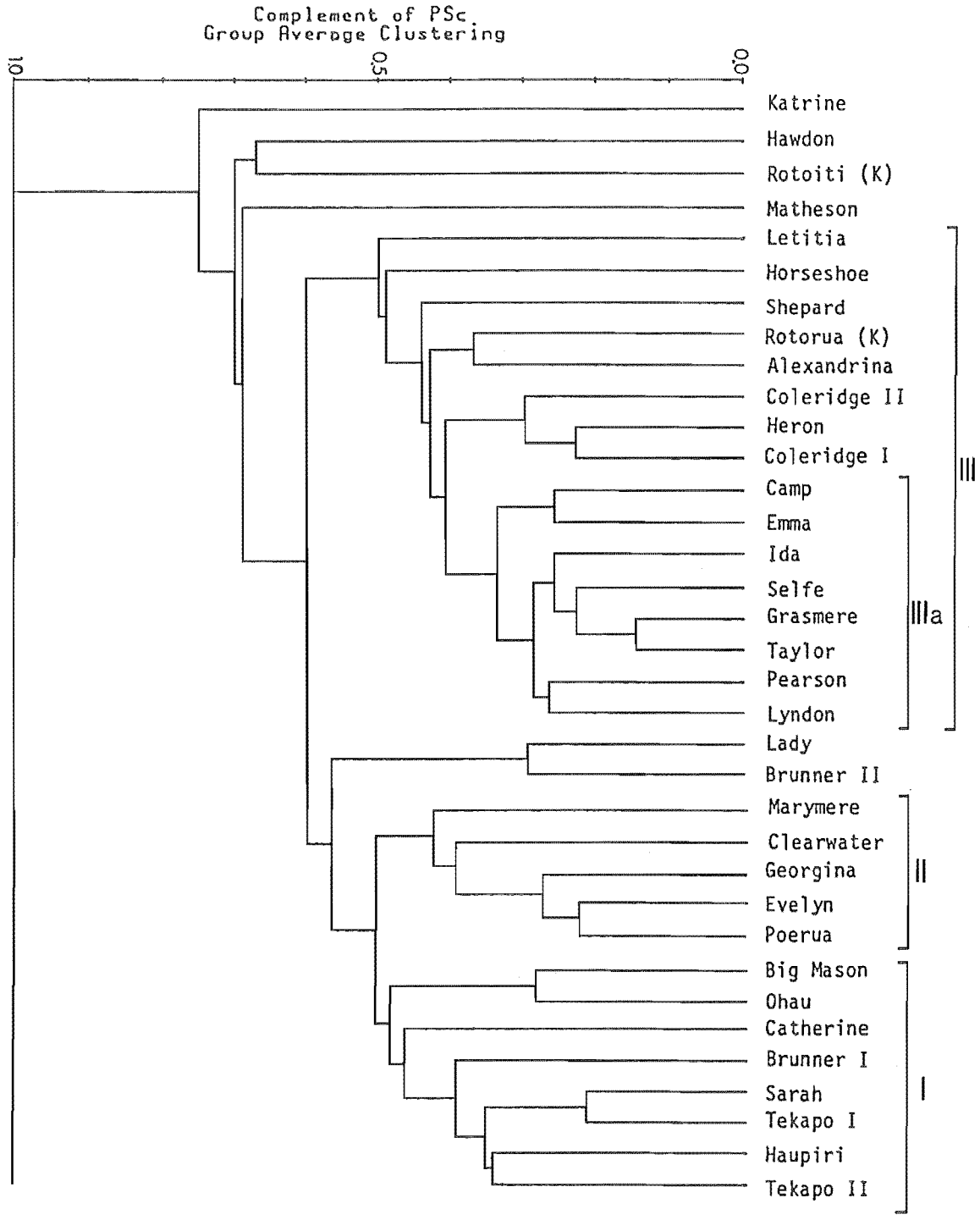


Fig. 8.5. South Island lakes: Dendrogram based on an average linkage cluster analysis on the relative abundance of the chironomid taxa in the surficial sediment samples. The vertical axis gives the values of the dissimilarity index. The group codes are indicated by Roman numerals.

Table 8.6. Two-way table of coincidence giving the mean relative abundances (%) of the Chironomidae taxa found in surficial sediment samples from South Island lakes in each sample cluster (Groups I-III), N = number of samples in each group (L/B = Lady Lake, Brunner I).

TAXON/GROUP	I	II	III	L/B
Chironomus	9.5	9.2	36.5	10.7
Paucispinigera sp.a	7.2	0.0	0.0	6.1
Polypedilum	1.1	0.8	1.5	1.0
Cladopelma	0.9	0.3	2.7	0.0
Chironomini sp. A	5.0	0.2	5.0	4.0
Corynocera	0.8	2.4	3.9	0.0
T. vespertinus	2.0	6.9	2.1	0.0
T. funebris	2.8	1.7	3.3	0.0
Paratanytarsus	1.5	1.2	1.8	0.0
Orthocladiinae sp. IX	21.3	51.9	13.4	17.1
Cricotopus	17.6	11.0	7.5	6.9
C. aucklandensis	1.8	1.5	2.9	5.9
Orthocladiinae VIII	0.3	0.3	0.9	1.0
Eukiefferiella	3.2	0.0	0.9	21.7
E. claripennis gr.	0.4	0.0	0.7	6.0
Apsectrotanypus	10.1	4.0	7.9	0.0
Tanypodinae sp. I	1.5	1.5	1.6	0.0
nr. *Pentaneura*	5.6	1.8	1.3	1.9
G. antarcticus	1.0	1.8	0.5	0.0
N	8	5	16	2

sub-dominant chironomid, although this taxon was not as abundant as in group I. The relative abundances of the Tanypodinae, especially that of Apsectrotanypus was low. Chironomini, and especially Chironomus, occurred in this group in their lowest abundances. Of the Tanytarsini, Tanytarsus vespertinus occurred with its highest abundance. Lakes in Group III possessed a chironomid fauna in which Chironomus was found with its maximum relative abundance. In most samples, this taxon was found with a relative abundance of >30%. Exceptions were Horseshoe Lake and Lake Letitia. The fauna in Horseshoe Lake was dominated by Cricotopus aucklandensis and Chironomus was found only with 23.5% relative abundance. Lake Letitia had an unusually high abundance of Corynocera (25.6%) and Chironomus occurred with a relative abundance of only 22.1%. Although these two lakes belonged into Group III, their position in the dendrogram marked them as outliers of this group.

The lakes which have not been assigned to a group have been separated from the remaining lakes because of high abundances of non-common taxa: Lady Lake and Brunner II had a high occurrence of Eukiefferiella, the abundances of E. claripennis, Orthocladiinae sp. IX and Paucispinigera sp. a were relatively high, and that of Chironomus was low; Lake Matheson's fauna was very different from most of the other lakes through the dominance of the fauna by Paucispinigera sp. a, and a very low relative abundance of Chironomus (2.4%); the fauna of Lake Rotoiti was dominated by Cladopelma; the fauna of Lake Hawdon was dominated by Tanytarsini, and that of Loch Katrine by Apsectrotanypus. Furthermore, a relatively high occurrence of Gressittius antarcticus was found in the latter lake.

To test these groupings, a correspondence analysis was carried out. The ordination of the 35 sediment samples based on the percentage distribution of the 19 species used in the classification analysis is shown in Fig. 8.6. The colour code denotes the abundant taxa in the samples which are responsible for the ordination result. The ordination diagram is based on the sample scores of the first two axes. The canonical correlation R (Orlóci, 1978) was R(X/Y)=0.5853 for Set 1 and R(X/Y)=0.5031 for Set 2.

In the ordination diagram most samples are placed rather closely together in the lower right and left quadrants. But the distribution of the most abundant taxa in the samples (as highlighted in the diagram by the colour code) shows some definite trends. The outliers are clearly identified and describe possible gradients. Lake Matheson (28) has the highest score on axis one and a high score on axis two due to the high abundance of Paucispinigera sp. a. Lake Rotoiti (10) has the highest score on axis two and the lowest score on axis one because of the dominant taxon in this sample, Cladopelma. Loch Katrine (29) with a low score on axis one and the lowest score on axis two has as the dominant chironomid Apsectrotanypus. Lake Marymere's fauna (4) is dominated by Orthocladiinae sp. IX and has a low score on axis two but a relatively high score on axis one placing the sample into the right lower quadrant together with most other samples with a relatively high proportion of Orthocladiinae sp. IX. Lakes with a high proportion of Chironomus in the fauna are concentrated in the lower left quadrant (group III) and those lakes with high abundances of

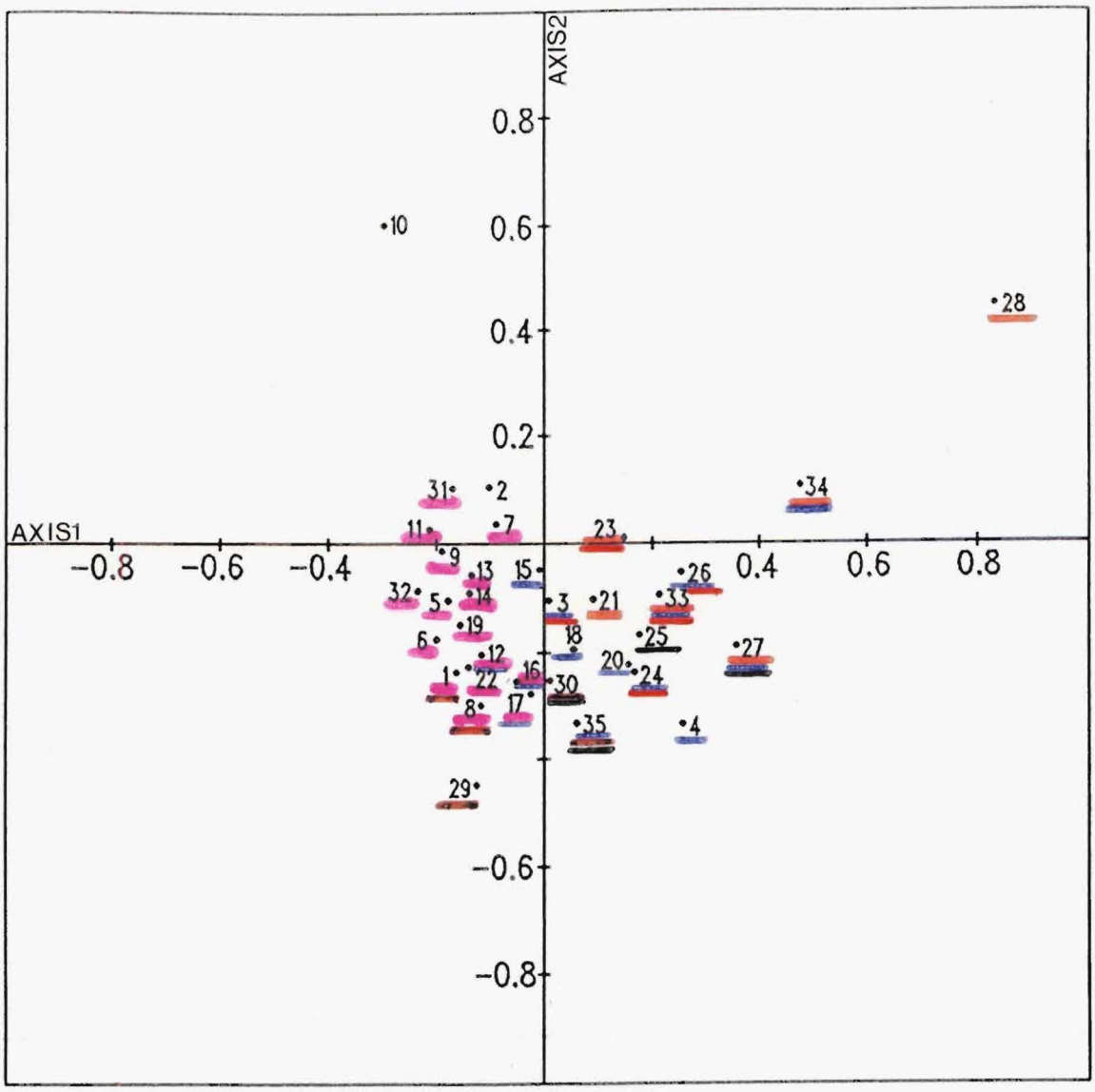


Fig. 8.6. South Island lakes: Reciprocal averaging ordination of surficial sediment samples. The analysis is based on the relative abundance of chironomid taxa in the samples. The colour code on the overlay denotes the dominant taxa in the samples: pink - *Chironomus*, blue - Orthocldiinae sp. IX, red - *Cricotopus*, brown - *Apsectrotanypus*, orange - *Paucispinigera approximata*, black - *Eukiefferiella*.

Chironomus which have been placed in the upper left quadrant have relatively high percentages of Tanytarsini in the fauna. These lakes include Horseshoe Lake (7, 14.7% Tanytarsini), Lake Rotorua (11, 18.5% T. vespertinus), Lake Letitia (31, 25.6% Corynocera) and Lake Hawdon (2, 42.1% Tanytarsini). Generally, the validity of the grouping based on the classification analysis has been supported by the ordination of the sites by the correspondence analysis, although the separation of the groups is not as clear as in the classification analysis.

8.5. Discussion

The composition of the fossil chironomid fauna in surficial sediment samples is influenced by two sets of processes: environmental factors determining the habitat and the population size of the species; and sedimentary processes, such as resuspension and redeposition. The effect of redeposition might be small in larger lakes (Iovino, 1975) but in smaller lakes, or depending on the specific lake morphology, might be considerable so that the faunal structure reflects conditions from other areas in the lake as well (e.g. the littoral area). Resuspension due to large storms, for example, can cause the mixing of younger with older sediments so that the fossil remains do not reflect only the very recent situation in the lake. Profundal sediments are less prone than littoral sediments to resuspension (Davis et al., 1985) but the mixing of sediments of differing ages can also be caused by animals living in the sediments. Therefore, the faunal assemblage recovered from surficial sediments might give information about a longer time interval than the most recent period of deposition.

In the discussion of the chironomid remains from surficial lake sediments an attempt will be made to determine which limnological factors have been responsible for the faunal structure of the chironomid assemblages, and whether it is possible to use these chironomid communities as analogues for fossil communities in cores.

The number of species in the surficial sediments of the lakes studied was higher than that recorded by Timms (1982, 1983) in his study of the benthos of 20 lakes in the South Island. Timms studied only the benthos beyond the macrophyte beds, whereas the chironomid taxa in the

surficial sediments included littoral and macrophyte-associated taxa. In Timms' study (1982) the species number was lowest in Lakes Ohau and Tekapo (only two species), whereas in the present study eight taxa were found in Lake Ohau and 11 in Lake Tekapo. The highest species number was recorded in dystrophic Lake Gault (9 species) by Timms (1982) and two of the dystrophic lakes included in this study also had the greatest number of species (Lakes Matheson (16) and Haupiri (23)). Species numbers in the surficial sediments were comparable to the numbers of fossil assemblages in the core from Lake Grasmere, where taxa numbers of up to 23 taxa per sample were found.

The numerical analyses based on the percentage composition of the fossil chironomid taxa in the surficial sediment samples placed the lakes in three groups and an outlier category. A comparison of the available limnological parameters of the lakes in these groupings might show common factors which influenced the composition of the chironomid fauna. It appears that lakes have not been grouped together because of lake size, maximum depth, sampling depth or geographical proximity. Group I contains most of the largest and deepest lakes included in this study, Lakes Ohau and Tekapo, and Lake Brunner on the West Coast, but also another smaller West Coast lake (Haupiri), a small Cass lake (Sarah), small Lake Catherine near Lake Coleridge and one of the lakes of the Hurunui River catchment (Lake Mason) (Tables 8.2. and 8.3). Maximum depths of the lakes in this group ranged from 129 m (Lake Ohau) to 5 m (Lake Catherine) and sampling depths ranged from 1.5 m (Lake Catherine) to 45 m (Lake Brunner I).

Lakes in group II contained only small lakes, Lake Marymere at Cass, Lakes Georgina and Evelyn near Lake Coleridge, one of the Ashburton lakes (Lake Clearwater) and Lake Poerua on the West Coast. The maximum depths of these lakes ranged from 3 m (Lake Evelyn) to 18 m (Lake Clearwater) and the sampling depths from 3 m to 17 m in the latter lakes.

Group III contained several lakes from the Cass region (Lakes Grasmere, Pearson, Lyndon and Letitia), Lakes Taylor and Sheppard in the Hurunui River catchment, Lake Alexandrina located beside Lake Tekapo, three of the Ashburton lakes (Lakes Heron, Camp, and Emma), Lakes Coleridge and nearby Selfe and Ida, as well as Horseshoe Lake

and one of the coastal lakes (Lake Rotorua). Most of the lakes in this group are small, except for Lake Coleridge; the maximum depths of these lakes ranged from 200 m (Lake Coleridge) to 3 m (Lakes Rotorua and Emma) and sampling depths from 0.3 m (Lake Rotorua) to 36 m in Lake Taylor. The most homogeneous group of lakes with regard to size, depth, sampling depth and geographical location appears to be subgroup IIIa (Tables 8.2. and 8.3.).

Of the lakes which were classified as outliers, Lady Lake is located relatively close to Lake Brunner, but the two lakes differ in size and water depth. The sampling depths in both lakes were similar (20 m in Lady Lake and 23 m in Lake Brunner). Lake Matheson, a small, relatively shallow lake, is located furthest to the south on the West Coast; Lake Rotoiti is a small and very shallow coastal lake near Kaikoura; Lake Hawdon, also shallow, is one of the Cass lakes, located adjacent to Lake Marymere; and Lake Katrine is one of the four lakes studied located in the upper Hurunui River catchment.

The trophic state of the lakes varied to some degree both within and between groups. In group I, lakes have been classified as oligotrophic (Lakes Ohau, Catherine, Tekapo; Livingston et al., 1986), dystrophic (Lake Haupiri; Paerl et al., 1979), oligo-to mesotrophic (Lake Mason) and mesotrophic (Lakes Sarah, Brunner) (Livingston et al., 1986). The chlorophyll concentrations of all lakes in this group (Table 8.4.) are characteristic of oligotrophic lakes (see White, 1983), although some of the water samples have been collected in winter.

Most lakes of group II have been classified as mesotrophic (Lakes Clearwater, Georgina, Evelyn; Livingston et al., 1986), Lake Poerua as dystrophic (Paerl et al., 1979) and Lake Marymere as oligo-mesotrophic. The latter lake had a low chlorophyll concentration (Table 8.4.), which was also found for Lakes Georgina and Evelyn. The water samples from the two latter lakes were collected in May and June (Table 8.4.).

Lakes of group IIIa have been placed in the oligo-mesotrophic category (Lakes Taylor, Selfe, and Letitia) or in the mesotrophic range (Lakes Pearson, Camp, Ida, and Emma) (Timms, 1983; Livingston et al., 1986), whereas Lake Grasmere appears to be eutrophic according to the

concentration of chlorophyll (Table 8.4.; and see White, 1983). The remaining lakes in group III are mesotrophic (Lakes Alexandrina and Sheppard) and eutrophic (Lakes Rotorua and Horseshoe), and these lakes had also relatively high concentrations of chlorophyll (Table 8.4.). Lakes Lyndon, Heron, and Coleridge were the only lakes in this group which have been classified as oligotrophic (Livingston et al., 1986) and had low chlorophyll concentrations (Table 8.4.).

The trophic state varied also within the group of outliers. Two of these lakes have been classified as dystrophic (Lakes Matheson and Lady Lake; Paerl et al., 1979), Lake Hawdon as mesotrophic (Livingston et al., 1986) and Lake Rotoiti as eutrophic (Stout, 1985).
It appears that the trophic state was not primarily responsible for the composition of the fossil chironomid fauna in the surficial sediment samples, as lakes which were grouped together on the basis of the percentage proportion of certain taxa differed to varying degrees in their trophic state.

Comparing the faunal composition of the most common taxa in lakes of group I, it can be shown that in most lakes of this group the most abundant faunal components belong to littoral taxa or taxa associated with macrophytes. Orthocladiinae sp. IX, a macrophyte shredder (see Chapter IV), was dominant or sub-dominant in most lakes in this group. Cricotopus, a littoral form, was dominant in Lakes Catherine and Haupiri, sub-dominant in Lake Brunner I, Sarah, and Tekapo I, and abundant in Tekapo II. Paucispinigera sp. a, which also prefers the littoral zone or shallow lakes (e.g. Lake Gault, Timms, 1982; living larvae were found by the author in the littoral zone of Lake Lyndon), but was dominant in Lake Tekapo II and abundant in Lakes Tekapo I, and Haupiri. Chironomids which can live in the profundal zone, e.g. Chironomus and Apsectrotanypus, had low abundances in this group. Although the lakes in this group differ in size and geographical location, these lakes were similar in two respects. Loss-on-ignition and Secchi disc readings were generally low (Tables 8.2. and 8.3.). Lake Sarah was the exception with a high amount of organic matter in the sediments (23%), but a relatively low Secchi disc reading (2.8 m). This lake would have fitted better in group II. It was placed probably in group I because the dominant taxon, Orthocladiinae sp. IX, occurred with a relative abundance of only 24%. The water transparency in Lake

Brunner I was relatively high (5.3 m) (as was that in Lake Brunner II), but loss-on-ignition was very low at both sampling stations (Table 8.2.). Lake Brunner II would fit into group I according to the dominance of littoral taxa but was associated with Lady Lake because of high abundances of an uncommon chironomid, Eukiefferiella sp. Lady Lake also had a strong littoral component amongst the dominant chironomids and a low Secchi disc reading which likewise places it close to group I. It appears that group I encompasses lakes which are generally unproductive due to low light penetration caused by either high turbidity (especially Lakes Ohau and Tekapo; Stout, 1978), or stained water (dystrophic Lakes Haupiri, Lady Lake and Lake Brunner; Paerl et al., 1979) with a small proportion of profundal chironomids. Timms (1982) also found the lowest standing crops in Lakes Ohau and Tekapo and the dystrophic West Coast lakes included in his study.

Paucispinigera sp. a occurred mainly in lakes of group I, in both the unproductive and dystrophic lakes (e.g. Tekapo, Ohau, Brunner, Haupiri, and Lady Lake) and was most abundant in Lake Matheson. This lake is also dystrophic and was the most acidic of all lakes studied, with a pH of 5.1. Therefore, this taxon might be restricted to the more unproductive lakes and can tolerate acidic waters. There appears to be another taxon with a similar but even more restricted distribution, Tanypodinae sp. II, which was found only in Lake Matheson in the present study. Both taxa also occurred in the fossil fauna of the unproductive Lake Monowai (Schakau, unpubl. data).

Lakes which belong to group II have a very high proportion of Orthocladiinae sp. IX and a relatively high abundance of Cricotopus, which live closely associated with macrophytes. The abundances of both Chironomus and Apsectrotanypus are at their lowest for the three groupings of lakes (Table 8.6.). The lakes included in this group are relatively small and shallow and generally contain a large amount of organic matter in the sediments. The composition of the fauna in the surficial sediments is a reflection of the extensive beds of macrophytes in these lakes which cover most of the lake floor in some of these lakes. In Lake Marymere, macrophytes grow down to 5 m (Timms, 1983), and in Lake Georgina only a small area around an underwater spring in the deepest part of the lake was free from macrophytes (pers. obs.). A high proportion of macrophytes in these lakes was also

indicated by the composition of the fossil diatom flora from surficial sediments (Harper, pers. com.). The fossil diatom flora in Lake Clearwater had a proportion of >40% epiphytic diatom species, and Lakes Evelyn, Georgina, and Marymere had a proportion of >50% epiphytic diatoms. Lake Poerua, a shallow, dystrophic West Coast lake, had the highest light penetration of the dystrophic lakes studied by Paerl et al. (1979), and therefore could have had possibly more growth of macrophytes than the other lakes (e.g. Lakes Brunner, Lady Lake, and Haupiri).

Most of the lakes of group III have been associated together because Chironomus was the dominant chironomid and occurred with a relative abundance of >30%. The most closely grouped lakes of sub-group IIIa had as the sub-dominant taxa generally Apsectrotanypus, Orthocladiinae sp. IX or Cricotopus, whereas the sub-dominant taxa in Lake Alexandrina were Chironomini A and Corynocera, in Lake Rotorua Tanytarsus funebris and Chironomini A, and in Lake Sheppard T. vespertinus and Paratanytarsus. Lakes of sub-group IIIa and Lakes Alexandrina, Rotoiti and Sheppard were generally more productive and had an organic matter content of the sediments between 9-20% of dry weight (except for Lake Ida, Table 8.2.). The relatively high abundance of Apsectrotanypus in some of these lakes pointed to a larger area of open mud than in lakes of group II, as larvae of this taxon are usually found beyond the macrophyte beds (see Chapter V). Apsectrotanypus remains were rare in the very shallow lakes and occurred only in Lake Catherine with a relative abundance of >10%.

The presence of macrophytes in most of these lakes is associated with the relatively high abundances of Orthocladiinae sp. IX and Cricotopus. Lake Alexandrina, which has macrophytes growing down to a water depth of 10 m (Ward & Talbot, 1984), had only low abundances of these two taxa. A similar result was found also for the Hurunui Lakes (Katrine, Mason, Sheppard and Taylor), which also have extensive macrophyte beds (De Winton et al., 1991) but relatively low abundances of Orthocladiinae sp. IX and Cricotopus. It is not known what caused this distribution of the two taxa in these lakes.

The lakes which differed the most from the other lakes in group III were Lakes Horseshoe and Letitia. The fauna of Lake Letitia was

dominated by Corynocera, and had Chironomus and Orthocladiinae sp. IX as the sub-dominant taxa. This lake had very clear waters (Secchi disc: 11 m) and flocculent mud (Timms, 1983), which appear to be conditions favoured by this taxon.

Eutrophic Horseshoe Lake was dominated by Cricotopus aucklandensis. Chironomus and Orthocladiinae sp. IX were the sub-dominant taxa. The water transparency in this lake was low and the dominant taxa contained a strong littoral element. Timms (1982) when studying the benthos of Lake Horseshoe found a different fauna with Chironomus dominant and Macropelopiini and Cladopelma curtivalva abundant. But in the fossil fauna Tanypodinae and Cladopelma were rare (Table 8.4.). The reason for this difference is not known. A possibility could be the frequent resuspension of littoral sediments which are then redeposited in the deeper area of the lake thereby diluting the remains of the profundal fauna.

Timms' (1982) study indicated that Cladopelma appears to prefer the more productive lakes. This taxon was rare in most surficial sediment samples but accounted for 40% of the fossil material in Lake Rotoiti. This lake was highly eutrophic and had the maximum concentration of chlorophyll in the lake water (Table 8.4.). One of the sub-dominant taxa in Lake Rotoiti was Tanytarsus funebris. This taxon also occurred with relatively high abundances in the eutrophic Lake Rotorua and in Lake Hawdon, which had the second highest standing crop of the lakes studied by Timms (1982). The occurrence of this taxon in these lakes might indicate a preference for the more productive but shallow lakes as Tanytarsini are littoral forms. Lake Hawdon had the highest proportion of Tanytarsini remains and was dominated by T. vespertinus. It is possible that the consistency of the sediments in this lake which were very firm but 'sticky' (Timms, 1983) provided a good substrate for Tanytarsini.

Loch Katrine had the highest proportion of Tanypodinae and was dominanted by Apsectrotanypus. Chironomus and Gressittius antarcticus were the sub-dominant taxa. Loch Katrine was the only lake in which the relative abundance of Gressittius was >10%. The reason for the dominance of Tanypodinae in this lake is not known.

Three lakes in group III, Lake Coleridge I and II, Lakes Heron and Lyndon, have been placed in this group because of high abundances of Chironomus with Orthocladiinae sp. IX as the sub-dominant taxon. All three lakes are oligotrophic, illustrating that species of Chironomus can also occur in unproductive lakes.

This example highlights one of the difficulties in evaluating the results of this type of analysis for the lakes in the South Island using different volumes of sediment from which the fossils are derived. Although the percentage composition of the fossil fauna might give an accurate picture of the trends in the dominance pattern of the fauna over a certain time of deposition, it does not necessarily give any information about the size of the original populations. Some of the more productive lakes in the South Island (e.g. many of the Cass lakes) have relatively high standing crops for their trophic state in comparison with overseas lakes (Timms, 1982, 1983). In these lakes a small amount of sediment will yield the necessary amount of head capsules, whereas in the very unproductive lakes large quantities might have to be examined. Thus, although the pattern of dominance might be the same, the size of the original population was not comparable. This was the case with the sediments from Lake Coleridge which contained a relatively low fossil density and more than 10 g of sediments were used for the analysis. The addition of counting absolute numbers of fossils in fixed sediment volumes would alleviate the problem of great variations in standing crops of chironomid taxa and these results are then more useful for the interpretation of fossil communities in cores.

To conclude, this study has provided some valuable information about the distribution of chironomid taxa in the South Island of New Zealand. It has also shown the necessity of more work on the taxonomy of chironomids and on the factors which regulate the distribution of the individual taxa. Some of the fossil assemblages in the surficial sediment samples were potentially useful as analogues for the fossil communities in the Lake Grasmere core, e.g. those from Lake Grasmere for the top sediments, from Lake Marymere for the 25-20 cm horizon in which Orthocladiinae sp. IX was dominant, and from Lake Letitia in which Corynocera was dominant.

8.6. Summary

The recently deposited chironomid remains in surficial sediments from 32 lakes in the South Island were studied to establish relationships between faunal assemblages and limnological conditions of the lakes studied. A classification analysis based on the relative abundance of 19 chironomid taxa separated three main groupings of lakes and identified four lakes as outliers. Lakes of group III were mainly mesotrophic with an organic matter content of the sediments ranging from 9-20% of dry weight. These lakes were dominated by Chironomus and had high abundances of either Apsectrotanypus or Orthocladiinae sp. IX. Lakes of group II were relatively shallow with extensive macrophyte covers and had relatively high percentages of organic matter in their sediments. The dominant taxon in these lakes was Orthocladiinae sp. IX. Group I included lakes with generally low contents of organic matter in the sediments and low Secchi disc readings due to high turbidity or colouring of the lake waters. These lakes did not have a prolific profundal faunal component. They were dominated either by Cricotopus and/or Orthocladiinae sp. IX. Larvae of these taxa originally inhabited the macrophyte zone of lakes and their fossil remains were transported into the deeper zones of these lakes prior to sedimentation. The lakes classified as outliers had high abundances of uncommon taxa. These high relative abundances could be related to unusual limnological features in some of these lakes, including high pH and chlorophyll content of the lake waters.

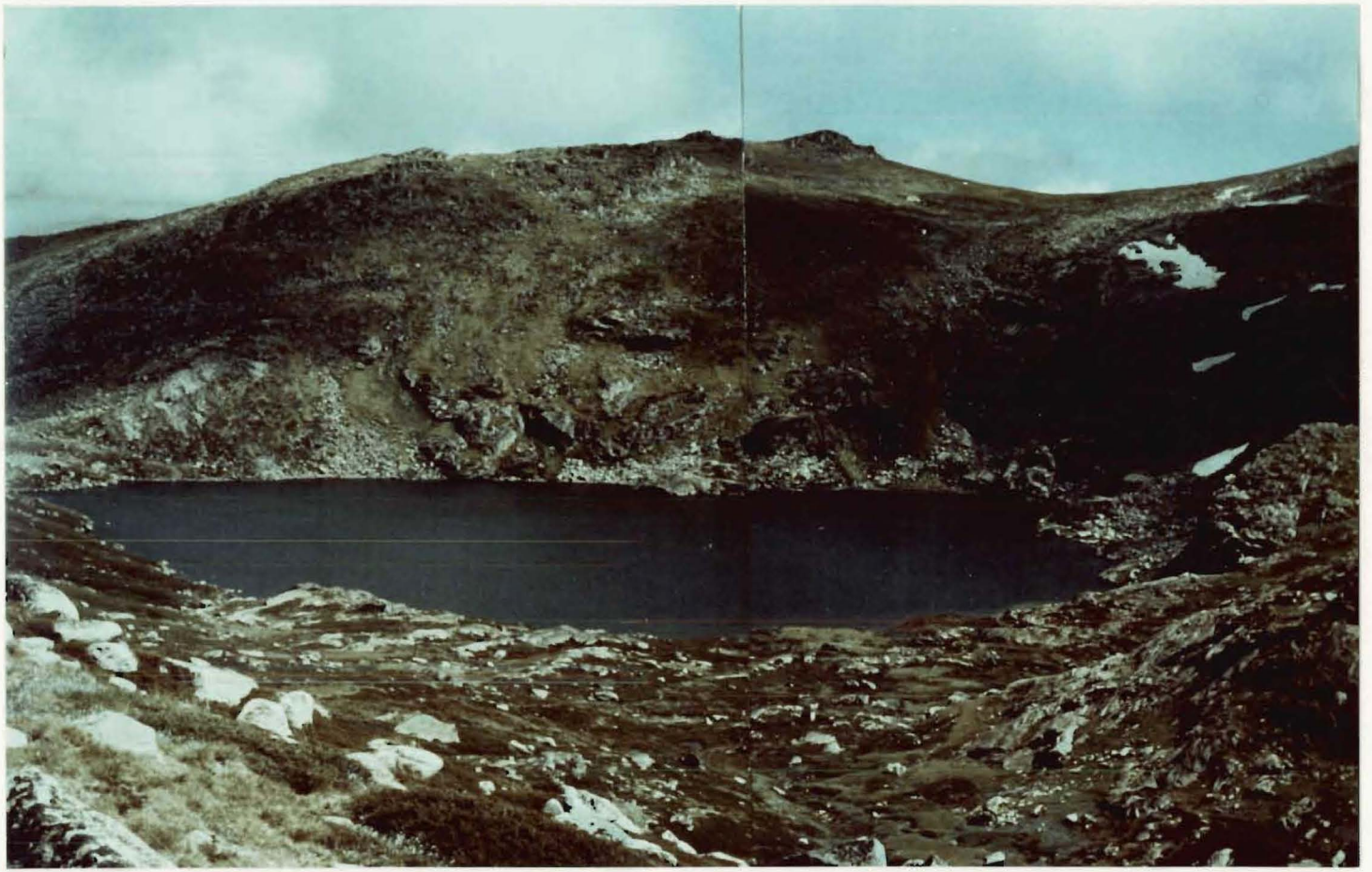


Plate 9.1. Blue Lake in north-east direction (March 3, 1987).

CHAPTER IX

THE SUCCESSION OF FOSSIL CHIRONOMIDAE IN BLUE LAKE, MT. KOSCIUSKO NATIONAL PARK, AUSTRALIA, DURING THE LATE PLEISTOCENE AND HOLOCENE

9.1. Introduction

In Australia several authors have drawn attention to the importance of palaeolimnological studies to monitor environmental change, develop sound management strategies for waterbodies or find past environmental analogues for climatic change (DeDeckker, 1982a; Clark & Wasson, 1986; DeDeckker, 1986; Longmore, 1986; DeDeckker et al. 1988). Most of the studies of lacustrine sediments carried out so far in Australia have dealt with the analysis of pollen sequences to reconstruct Quaternary environments (Kershaw, 1973; Raine, 1974; Singh, 1981; Martin, 1986; D'Costa, 1989; Edney et al., 1990), chemistry of lake sediments (Longmore, 1986), diatoms (Yezdani, 1970; Croome & Tyler, 1973; Tudor, 1973) or ostracods (DeDeckker, 1982b, 1983). Ostracod remains preserve well in sediments of saline lakes, and as most of mainland Australia is dominated by saline waterbodies, the study of fossil ostracods reveals important information about the past conditions of these ecosystems, such as water depth, temperature and salinity (Chivas et al., 1986). However, although DeDeckker (1982a) mentioned the potential of fossil chironomid analysis (albeit more for saline waters), the only work is that of Paterson & Walker (1974) on the distribution of two chironomid species from a short core.

In the present study the first long-term record of the development of the fossil Chironomidae fauna from a freshwater lake in Australia is described. The sediment core studied was derived from Blue Lake in the Snowy Mountains. Blue Lake is an unusual lake in the context of waterbodies on mainland Australia. It is an alpine lake located above the forest limit (Thomasson, 1956; Costin, 1981), of glacial origin, extremely dilute in chemical content (Williams et al., 1970; Balmaks, 1984), dimictic (Raine, 1982) and during most of its history was little influenced by anthropogenic activities (Costin et al., 1980). The choice of Blue Lake for the present study therefore fulfills two

objectives: to provide baseline data of faunal development of fossil chironomids against which the composition of fossil chironomids from different types of freshwater ecosystems in Australia can be compared; and to compare the succession of fossil chironomids in Australian glacial lakes with that of glacial lakes in the South Island of New Zealand.

9.1.1. The Chironomidae of Australia

In the Australian Chironomidae, seven subfamilies are distinguished: Tanypodinae, Chironominae, Orthocladiinae, Podonominae, Diamesinae, Aphroteniinae, and Telmatogenoninae (Cranston & Martin, 1989). The major systematic studies of the chironomids of Australia are those by Freeman (1961), Glover (1973), Hergstrom (1974), and Roback (1982a, b). Freeman (1961) revised the adult taxonomy of the family describing 129 species, 69 of them new, spanning 51 genera. The taxonomy of the adult Tanytarsini was dealt with by Glover (1973) who provided descriptions of 46 species, 33 of them new, in six genera. Hergstrom (1974), who sampled the wetter regions of South Australia, provided decriptions of 70 new species of Orthocladiinae, one new species of Aphroteniinae, and two species of Heptagyini. Adult Tanypodinae, and in some cases immature stages, of 19 species were described by Roback (1982a, b). The most recent list of the Australian chironomid fauna is given by Cranston and Martin (1989). According to their catalogue, the Australian chironomid fauna consists of 198 species in 86 genera.

As with the Chironomidae of New Zealand, the Australian chironomid fauna is comprised of three faunal elements: cosmopolitan genera, genera showing affinities with South America, and endemic genera (Edward, 1986). Eleven endemic genera occur in Australia: Coelopynia (Tanypodinae); Allometriocnemus, Allotrissocladius, Austrobrillia, Nasuticladius, Doloplastus, Kiefferophyes (Orthocladiinae); Megacentrum, Paraborniella, Imparipecten, and Parvitergum (Chironominae) (Cranston & Martin, 1989).

The common cosmopolitan genera belong mostly to the Chironominae and Tanypodinae, and to a lesser extent to the Orthocladiinae. Generally, the cosmopolitan genera of Orthocladiinae are found in lotic waters,

whereas the cosmopolitan species of Chironominae and Tanypodinae colonize mainly lentic waters, where they are often the most prominent invertebrates. Most of these species can be found also in lotic waters (Edwards, 1986; Pettigrove, 1990).

Some of these genera have northern affinities and represent the more recent elements in the Australian chironomid fauna (Winterbourn, 1980). New Guinea and adjacent areas are considered as areas of origin for parts of the Australasian aquatic insect fauna. Their dispersal might have been either by air or along past land connections. The meeting of the Austalian and Asian plates (Raven & Axelrod, 1972) 10-20 m.y. ago was the beginning of the mixing of Oriental (Indo-Malaysian) and Australian taxa. A system of island arcs migrating southwards probably conveyed a biota derived from Asia to Australia (Talent, 1984).

Chironomid genera with an amphinotic (= circum-Antarctic) distribution are found in the Podonominae, Aphroteniinae, and austral Heptagyini (Brundin, 1966). These groups include the most primitive species, being at least 150 m.y. old. Brundin (1965, 1966) showed that these cold-adapted, mostly rheophilous groups have close relatives either in South America or South Africa. Thus, these groups of chironomids are thought to be derived from an old Gondwanaland fauna whose vicariance has been brought about by continental drift since the Mid-Jurassic (Norton, 1982).

9.1.2. The Distribution of Chironomidae in Australian Lakes

Several studies of the benthos of freshwater lakes in Australia (see Timms, 1980b), have shown that Chironomidae are often the most abundant faunal element whether as numbers of individuals per square metre or biomass. Compared with similar lakes in the northern hemisphere, the species diversity in Australia appears to be generally lower (Timms, 1980b; Winterbourn, 1980).

The commonly found chironomids inhabit most lakes so far studied (Timms, 1974b, 1980b, 1981). Procladius villosimanus is ubiquitous, Cladopelma curtivalva is widespread, and Chironomus duplex is mainly restricted to, and characteristic of the more productive lakes.

Valley Lake, Lake Leake and Lake Edward in the Mt. Gambier District, South Australia, had populations of Procladius villosimanus, and Chironomus duplex. Additionally, Cladopelma curtivalva was abundant in Valley Lake, and Ablabesmyia notabilis and Tanytarsus paskevillensis were present in L. Edward (Timms, 1974a). C. duplex had the highest biomass in L. Leake. Of the three lakes, L. Leake had the highest value of percentage total carbon in the mud. Except for Dicrotendipes conjunctus and Tanytarsus paskevillensis, which were confined to the littoral or sublittoral zone, all chironomid species occurred at all depths of the lakes studied.

Timms (1974b) recorded five chironomid species in Lake Tali Karng, the only deep, highland lake in Victoria (water depth 51 m). The benthos was dominated by three species of chironomids in the sublittoral (Ablabesmyia sp., P. villosimanus and Riethia stictoptera) and by Chironomus oppositus in the profundal. The profundal biomass almost entirely consisted of C. oppositus, a species which occurs mainly in muddy sediments. The chironomid fauna of L. Tali Karng has two distinct features: one group of species is widespread in lakes in south-eastern Australia (e.g. P. villosimanus), whereas the other is more characteristic of oligotrophic-mesotrophic lakes in Tasmania (e.g. Riethia stictoptera).

Chironomids are the most diverse group of benthic invertebrates in Tasmanian lakes. Timms (1978) found 11 species in Lake St.Clair. Common widespread species present in Tasmanian lakes included Coelopynia pruinosa, P. villosimanus, C. oppositus and Riethia spp. In the seven lakes studied by Timms (1978) five unidentified species of orthoclads were recorded with 1-2 species in every lake except for L. Crescent. In a later study of the benthos of three Tasmanian lakes, Fulton (1983a,b) found relatively high diversities and abundances of profundal chironomids. In Great Lake, 14 chironomid species were recorded. The major taxa were Riethia sp., Coelopynia pruinosa, P. villosimanus, and common taxa included Polypedilum nr. tonnoiri, and Tanytarsus sp. The composition of the chironomid fauna of Arthurs Lake (15 species) and of Lake Sorell (11 species) was similar to that of Great Lake with three additional species being abundant (Dicrotendipes sp. and C. curtivalva in Arthurs Lake and Cryptochironomus griseidorum in L. Sorell).

The four glacial lakes of mainland Australia, Blue Lake, Lake Cootapatamba, Lake Albina and Club Lake all had a very low chironomid diversity (Timms, 1980c). None of the lakes had more than three species. P. villosimanus and C. oppositus occurred in every lake, the latter species being abundant in Blue Lake and Club Lake. C. oppositus was only found as a dominant species in Lake Tali Karng and was common in the Tasmanian lakes.

The coastal dune lakes which lie on sand and contain acid waters with high concentrations of total dissolved solids, had a very depauperate chironomid fauna or were not colonized by chironomids at all (Timms, 1972). In the littoral zone of Lake Boemingen, a shallow subtropical lake on Fraser Island, the aphroteniid Anaphrotenia lacustris was highly abundant (Bayly et al., 1975). Fraser Island is the largest sand island in the world consisting almost entirely of siliceous sand. L. Boemingen is the largest lake on the island, and has a pH of less than 5 and an average surface temperature of 25°C. A. lacustris had been the only Aphroteniinae species that is not confined to lotic, and relatively cold waters (Brundin, 1983). Brundin suggested that the unique development of closely set papillae covering the body increases the surface area and facilitates oxygen uptake. Later studies by Cranston and Edwards (1992) indicated a wider range of habitats for Aphroteniinae in Australia showing that such taxa need not be cool-stenotherms restricted to the elevated areas of the South-East of the continent.

Lakes Barrine and Eacham, maars on the Atherton Tableland in North Queensland, were both dominated by Procladius sp., Ablabesmyia sp., and Chironomus nepeanensis. Dicrotendipes sp. was abundant in Lake Eacham and Conochironomus sp. in Lake Barrine (Timms, 1979).

In Western Australia, the chironomid fauna of the shallow Lake Monger contained seven chironomid species whose ecology and distribution were studied in detail by Edward (1964): P. villosimanus (active swimmer, predator), Cricotopus albitibia (inhabitant of algal mats around the lake, algae feeder), Chironomus australis (sediment-dwelling, detritus feeder), C. alternans (inhabitant of algal mats and surface layer of sediment, feeding on detritus and filamentous algae), C. conjunctus (colonizes algal mats, algae feeder), Polypedilum nubifer (sediment

dwelling, feeding on phytoplankton and detritus), and Tanytarsus fuscithorax (tube builder in the littoral zone).

In a waterfowl breeding habitat in south-western New South Wales, Murrumbidgil Swamp and Lake Merrimajeel, 12 species of chironomids were recorded (Maher and Carpenter, 1984). This is one of the highest recorded species diversities on mainland Australia. The most common species in the mud habitats were Chironomus 'alternans a', C. tepperi, Kiefferulus intertinctus, Polypedilum nubifer, Cladopelma curtivalva, Tanytarsus sp., and P. villosimanus. Procladius and Polypedilum showed a preference for the open water of L. Merrimajeel. No species of Orthocladiinae were recorded.

Chironomus alternans Freeman has been divided on cytological differences (Martin, 1971) into three species: C. cloacalis, C. februarius, and C. oppositus.

As the examples listed above show, the species diversity of Chironomidae in lakes on mainland Australia is generally low, whereas Tasmanian lakes possess a slightly more diverse chironomid fauna. After comparing the species richness of the profundal zone of lakes in Australia with that of comparable Holarctic lakes, Timms (1985b) concluded that the lower species richness of benthic macro-invertebrates in Australian lakes is largely a consequence of the small numbers of chironomid and bivalve taxa. It was suggested that the reason for this low diversity might be limited speciation on a landmass lacking large, permanent lakes with varied microhabitats. This argument might be supported by the generally higher diversity of chironomids in Tasmanian lakes where a greater number and variety of permanent lakes is found. Another explanation might be that species often need to be generalists (e.g. with regard to habitat or food) rather than specialists if there is a lack of well defined seasonal changes. Many chironomids found in Australian lakes are generalist feeders and are adapted to a wide range of conditions (Edward, 1964; Timms, 1980b). Contrary to the generally low chironomid diversity in Australian lakes, 29 benthic chironomid species were recorded in four permanent freshwater lagoons (billabongs) in the Magela Creek catchment, Northern Territory (Outridge, 1987). Two factors that might have caused this high species diversity are rarefaction (the removal

of organisms through predation and/or environmental disturbance, and therefore preventing dominance of species) and predictable environmental heterogeneity. Both mechanisms are directly related to the annual monsoon rainfall regime in this region of Australia (Outridge, 1987).

9.2. Description of the Study Area

Blue Lake (Plate 9.1.), near Mt. Kosciusko in the Snowy Mountains of New South Wales, is one of the highest lakes (1890 m a.s.L.) on mainland Australia. It is located at latitude 36° 25'20" South and longitude 148° 18'48" East. The lake occupies the lower basin of a two-storeyed cirque to the south of Mt. Twynam and was formed as a result of glacial activity (see Table 9.1.).

9.2.1. Palaeoecology and Palaeoclimate of Mt. Kosciusko National Park

During the last glaciation on mainland Australia, cirque and short valley glaciers covered only about 50 km^2 between Mt. Kosciusko and Mt. Twynam (Galloway, 1963). The period of greatest temperature reduction was between 25,000 and 15,000 yr B.P. in Australia. During this period climatic conditions were probably drier than at any other period in the last 50,000 years (Bowler et al., 1976).

This last glacial episode with glaciations occurring in New Guinea, Tasmania and on mainland Australia was equivalent to the late Würm-Wisconsin glaciation of the northern hemisphere. However, while the glaciation chronologies from the humid New Guinea and Tasmanian mountains closely agreed with some European sequences, the ice retreat from south-eastern Australia began earlier than in New Guinea, Tasmania and the northern hemisphere. Evidence from New Guinea indicated that the maximum refrigeration occurred between 18,000 and 16,000 yr B.P. (Bowler et al., 1976).

The data from the Snowy Mountains showed that temperatures rose rather than fell during that time. The first appearance of deglaciation on mainland Australia was in the period between 17,500 and 16,000 yr B.P. and ice retreat was well advanced by 13,000 yr B.P. (Bowler et al.,

1976). The ice retreat in the Snowy Mountains coincided with the period of major aridity, dune building, and drying of lakes in lower altitudes in south-eastern Australia after 20,000 yr B.P. (Rognon & Williams, 1977). After 13,000 yr B.P. vegetation recolonization occurred both at low and higher altitudes, which apparently reflected an amelioration in temperature and water balance (Bowler et al., 1976). According to Kershaw et al. (1983), temperatures were at least 5°C below present until 11,000 yr B.P., as indicated by the presence of alpine vegetation around Jackson's Bog in the south-eastern highlands until that time. The general increase in both rainfall and temperature during the early Holocene reached a peak between 7000 and 5000 yr B.P. This phase was associated with widespread global warmth. Conditions thereafter were colder and drier. The climate of the late Holocene was not substantially different from that found today. In the south-eastern highlands, a cold phase occurred between 3800 and 1700 yr B.P. During this period, mean annual temperatures were probably 2°C to 3°C lower than at present as implied by the development of periglacial features (Costin, 1972).

9.2.2. Pollen Sedimentation in Blue Lake

According to Raine (1974), the maximum depth of post-glacial sediment observed in cores was 7 m in the central basin (water depth 26 m). Organic sedimentation started in Blue lake around 13,000 yr B.P. Microfossils which originated in the lake appeared at this time, including 'Sphere-R' and 'Sphere-W'(unidentified phytoplankton taxa) marking the beginning of the existence of a lacustrine environment. About 10,000 yr B.P., the freshwater algae Botryococcus braunii and Baltisphaeridium sp., as well as 'Sphere-F' and 'Sphere-P' (possibly Trochiscia sp.) appeared. Except for Botryococcus, these taxa were not recorded continously during the entire developmental history of Blue Lake (Raine, 1974).

Raine (1974) recognized 5 pollen zones in the vegetation history of the Kosciusko area (data for the oldest zone were derived from a core taken in Twynam Cirque, above Blue Lake, ranging in age between 20,000 and 9000 yr B.P.).

Zone I (ca. 20,000 - 13,000 yr B.P.): Pollen derived from an alpine plant community occurred at increasing frequencies and included Ewartia sim. and Cruciferae; the former indicating feldmark (Epacris-Chionohebe alliance), the latter an increase in short alpine herbfield towards the close of the period.
Zone II (ca. 13,000 - 8700 yr B.P.): Short alpine herbfield taxa had their highest relative pollen frequency; pollen of fen community plants increased through the zone.
Zone III (ca. 8700 - 6500 yr B.P.): In this zone a great increase in total pollen deposition occurred. Alpine and common forest taxa increased at the base of the zone. Wet sclerophyll forest taxa (Pomaderris and Dicksonia) increased slightly later (7700 yr B.P.).
Zone IV (c. 3800 - 6500 yr B.P.): Total pollen deposition decreased. Pomaderris declined markedly.
Zone V (c. 3800 yr B.P. - present times): Pomaderris and Astelia declined markedly in this zone.

Based on his pollen analysis, Raine (1974) described the vegetation history of the Blue Lake area as follows: Little alpine vegetation occurred before 17,000 yr B.P. Then, short alpine herbfield entered the Twynam cirque. By about 13,000 yr B.P., the vegetation of the Kosciusko Plateau consisted of short alpine herbfield and feldmark communities with local areas of fen indicating climatic amelioration with a reduction in seasonal snow cover. The most significant change in climate occurred about 8700 yr B.P. Temperatures rose so that herbaceous plants were replaced by wet sclerophyll forest taxa as the treeline was raised from probably very low levels to its present position of 1750 m. The rise in temperature was accompanied by increased precipitation. Taxa of wetter habitats reached their maximum extents and importance between 7700 and 6500 yr B.P. Precipitation began to decline about 6500 yr B.P., and declined further at 3800 yr B.P. Raine (1974) suggested that the decline in precipitation was correlated with a cold phase, as evidenced by the presence of periglacial features. Precipitation appeared to have increased slightly since 1500 yr B.P.

9.2.3. The Present Climate

The mean annual temperature at Kosciusko Hotel, 10 km to the east of the Snowy Mountains, is 6.3°C, July is the coldest month and either January or February are the warmest months. Mean monthly temperatures at Kosciusko Hotel range from - 0.2°C in July to 12.0°C in February (Raine, 1974; data from the Bureau of Meteorology, 1969). Mean annual rainfall at Kosciusko Hotel is 1238 mm. The most reliable precipitation occurs during the winter. At the high altitude of Blue Lake, precipitation during winter is received mainly as snow which remains on the ground throughout the winter. The snow cover usually reaches 3 m, but 7 m has been recorded during a winter with exceptionally heavy snowfall. On exposed situations in the catchment of Blue Lake snow patches may persist through the summer months (Raine, 1974).

9.2.4. Blue Lake: Morphology and Catchment

Blue Lake (Fig. 9.1.) is partially dammed by a moraine (Dulhunty, 1945). Outcrops of granite in the bed of the efflux creek about 50 m downstream from the lake and 5 m below its surface show that the lake originated principally through glacial overdeepening of the valley floor. The moraine which partly dammed the lake, consists of five ridges running north-west and southeast parallel to the main trend of the valley. These ridges extend below the present shoreline (Raine, 1974). The rise which separates the two main sub-basins of the lake also bears ridges with a similar orientation. Dulhunty (1945) suggested that the ridges on the moraine dam, and those of greater depth on the lake floor, were built up by medial-morainic material resultingthe ridges on tuence of glaciers from the Crummer Range, upper Blue Lake Cirque, and the valley to the south of the lake.

Bathymetric maps (Fig. 9.1.) of Blue Lake are given by Dulhunty (1945) and Raine (1974, 1982). The lake has two basins, one occurring near the centre (26 m water depth) and one at the south-eastern end (28 m water depth). The lake is roughly trapezoidal in shape, 540 m long by 360 m wide. The present surface area is 1.44×10^5 m^2. Water level of the lake varies through the year by less than 1 m (Raine, 1974).

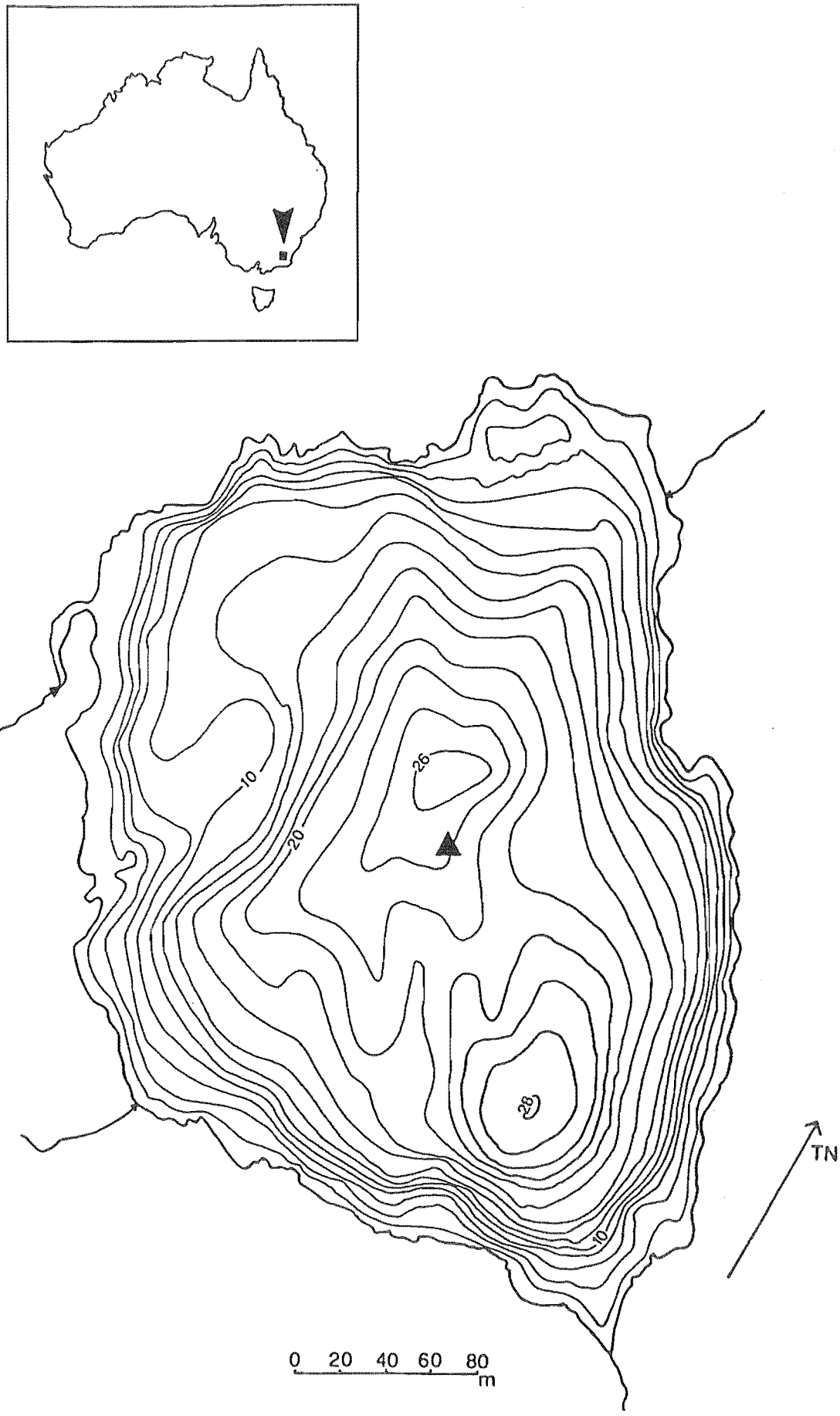


Fig. 9.1. Bathymetric map of Blue Lake (Contour Interval: 2m). The coring site is indicated by the black triangle (modified from Raine, 1974). The inset shows the location of the lake in Australia.

Shoreline development is minimal. The lake has three inlets, each with a small delta. The largest delta is situated at the entrance of the main creek on the western side. The deltas have only slightly modified the shape and volume of the lake. Except where the shoreline is composed of deltaic sediments, the lake bed is rocky to a depth of at least 7 m.

The surroundings of the lake show a northward-tending bedrock ridge on the southwestern side. Situated to the west is the delta of the largest influent stream (Blue Lake Creek). Progressing clockwise around the lake, steep slopes occur to the west until the entrance of a stream entering Blue Lake on the north-eastern side is reached. The relatively steep slopes extending from the stream entrance to the bedrock ridge are more vegetated than the rocky slopes on the opposite side (Raine, 1974).

The vegetation of the catchment of Blue Lake consists of Short Alpine Herbfield among the moist rocks of the cliffs, and outcrops around the lake with the typical dominants of the low growing Neopaxia australasica, Plantago spp., Caltha intoloba, Ranunculus spp., Dichosciadium ranunculaceum, and Oreobolus spp. An extensive area of Chionochloa tall alpine herbfield occurs on the northern side of Blue Lake. This is a distinctive tussock grass community which includes the snow daisy Celmisia longifolia and snow grass Poa caespitosa together with the associate Aciphylla glacialis (Apiaceae). On the south-eastern side, snowpatch feldmark occurs, and is dominated by cushion plants (Colobanthus spp). They are confined to freely drained, rocky, upper snow-patch situations where snow lasts for most of the year. The south-western side of the lake is dominated by tall heath. A variety of shrubs are common, e.g. Prostanthera cuneata, Grevillea spp., Phebalium spp., Orites lancifolia, Drimys xerophila, Oxylobium spp., Olearria spp., and Pimelea spp. Podocarpus lawrencei grows typically in rocky exposed situations (Raine, 1974).

On the ridges and saddles around Blue Lake, the plant community is windswept feldmark with the main dominant taxon Epacris microphylla, and in a few locations Epacris petrophila (Raine, 1974).

9.2.5. Anthropogenic Influences

Humans have lived in Australia for at least the last 32,000 years (Barbetti & Allen, 1972). During most of Blue Lake's history, the lake was scarcely influenced by human activities. The harsh and cold climate of the late-Pleistocene may have kept the Aboriginal people out of the mountain areas until conditions improved at the beginning of the Holocene (Mulvaney & Golson, 1971). Alpine areas appear not to have been permanently occupied by Aborigines. Only during the summer months, when the annual migration of the Bogong Moth (Agrotis infusa) occurred in the Mt. Kosciusko area (Common, 1954), did Aboriginal tribes (the Ngarigo of Monaro and the Omeo tribe from Victoria) move to the mountains to hunt the moths (Tindale, 1966; Flood, 1973). Overall, the effect of the Aboriginal people on the alpine environment was minimal.

Following the arrival of European people in Australia, the Kosciusko area was visited in the 1830s by explorers and local stockmen (Costin et al., 1980). The Kosciusko Plateau was one of the first areas to be used as a run for grazing cattle, and by the end of the century summer grazing of sheep and cattle with burning of the vegetation to promote fresh regrowth had become a well-established practice at Kosciusko. As a result of these actions, erosion was widespread and the rate of water retention in the highlands was reduced. Other uses of the Kosciusko area included tourism and the construction of dams for the provision of hydroelectricity and irrigation (Snowy Mountains Hydro-Electric Power Act of 1949).

The effects of human disturbance can be seen locally, as in the cirque above Blue Lake where relatively young peats are being buried by erosion debris from adjacent slopes (Costin, 1972). Lake and Marchant (1990) described the degradation of Australian upland streams as a result of human activity.

In 1944, the Kosciusko area was proclaimed a national park and in 1958 grazing was banned in the park in all areas above 1370 m (Costin et al., 1980). Hydroelectric works were stopped in 1972, and now the Mt. Kosciusko National Park is used mainly as a recreational area, and human impact on Blue Lake is limited to bushwalking.

The importance of preserving, restoring and/or rehabilitating the aquatic environments of the Mt. Kosciusko National Park has been noted by Leaver and Turner (1983), Balmaks (1984) and Lake and Marchant (1990). All authors indicated the lack of sufficient ecological research concerning the area. Studies of the benthic fauna of the alpine waters of Kosciusko National Park are necessary for establishing baseline information which should assist in determining the impact of management practise on aquatic biology (Leaver & Turner, 1983).

9.2.6. Limnology of Blue Lake

9.2.6.1. Introduction

Despite Blue Lake's geographical location (Table 9.1.), which makes access to the lake difficult, some data, collected on single visits, have been obtained on its chemistry (Williams et al., 1970), phytoplankton (Powling, 1970), zooplankton (Bayly, 1970), and zoobenthos (Timms, 1980c). There have been two seasonal studies on Blue Lake; one is Raine's (1982) report on the thermal regime of Blue Lake, and the other is a study of the limnology and bacteriology of the lake over a period of seven months (Balmaks, 1984).

In this study, sampling of the lake was undertaken to obtain information on the present-day chironomid fauna of the littoral and benthic regions of the lake. Physico-chemical data were also collected for comparison with the results of the previous limnological studies.

9.2.6.2. Methods

Water samples for chemical analyses and biological samples were taken by the author from Blue Lake on March 3, 1987. Conductivity and pH were determined at the lake using glass-electrodes. Oxygen concentrations were measured in the field by the Winkler method using a Merck field-kit (Aquamerck Sauerstoff, Nr. 11107, Methode Titrationsverfahren nach Winkler). Water samples were collected in poly-ethylene bottles and frozen for transport to the laboratory.

Phosphorus and nitrogen concentrations were determined by the State Laboratory, Rural Water Commission (Lab.-No. 1168, March 6, 1987).

Samples for chironomid larvae were collected from the littoral and profundal areas of Blue Lake. Littoral samples were taken with a hand-net from the shore around the lake and the main inlet at the western corner of the lake. The profundal samples were collected with an Ekman-grab from an inflatable boat at water depths ranging from 6 to 20 m (Table 9.2.). Because a very strong wind was blowing from the north-east, all profundal samples were collected from the north-western part of the lake. Samples were sieved and pre-sorted in the field. The pre-sorted samples were cooled for transport and the final sorting was carried out in the laboratory. Zooplankton and phytoplankton samples were taken from the boat with a phytoplankton net (mesh size 60 µm) by horizontal hauls. Rotifers were identified according to Ruttner-Kolisko (1974) and Shiel and Koste (1979).

9.2.6.3. Physico-chemical Features

Raine (1982) studied the thermal regime of Blue Lake from March 1971 until April 1972. His temperature profiles indicated a dimictic thermal regime. Epilimnetic temperatures were highest in late February and early March. Complete mixing began in April and continued until permanent ice formation occurred in June. During ice cover, lake temperatures were uniformly 1°C except close to the sediment-water interface, where temperatures of 2°C were measured. Ice cover lasted until November and all ice disappeared in December. By late January, summer stratification was established with a hypolimnetic temperature of 6.7°C. The approach of autumn turnover was indicated by decreasing epilimnetic temperatures and a deepening thermocline in April. Late summer stratification was also noted by Timms (1980) but not by the author (11.2°C at surface and 10.9°C at 20 m (Table 9.1.)). Balmaks (1984) inferred from the results of his study that the predominance and strength of stratification would depend upon the prevailing climatic conditions and consequently could vary from year to year. This suggestion has been corroborated by the results of this study, which was undertaken during very windy weather causing

Table 9.1. Blue Lake: Location, Morphometry, and Physico-chemical Features.

Location	36° 25′ S	Area	15.78 ha
	148° 19′ E	Max. Depth	28 m
Altitude	1890 m a.s.l.	Origin: glacial	

Beginning of lacustrine sedimentation: ca. 13000 yr BP

Physicochemical Features/ Sampling Date	10/7/1969 (1)	23/2/1984 (2)	3/3/1987 (3) Surface Water	Bottom Water
Secchi Disc (m)			4.50	
Temperature (°C)		13.7	11.2	10.9
Oxygen Saturation (%)			91.8	74.0
pH	6.05	6.56	6.25	6.1
Conductivity (µS/cm at 18°C)	5.00	6.56	31.6	20.5
Phosphorus, reactive as P (ppm)	0.009	<0.02	0.003	<0.003
Phosphorus, total as P (ppm)			0.012	
Total Kjeldahl Nitrogen (ppm)			0.15	
Nitrate + Nitrite (ppm)	<0.005		0.016	<0.003

Chemical Data from (1) Williams et al. (1970), (2) Balmaks (1984), and (3) author's unpublished data.

extensive mixing of the lake waters and obliterating any stratification, which Raine had found still persisted in March.

Physico-chemical features of Blue Lake waters are summarized in Table 9.1. The data from Balmaks (1984) are for the time of year closest to the authors's sampling date. During the author's visit to the lake, the weather was stormy, and the water was highly turbid. These conditions may have been the major reason for the relatively low Secchi disc reading (6 m was recorded by Timms, 1980c) and high oxygen saturation of the lake waters. Blue Lake was extremely fresh with a salinity < 3 ppm on 7 October 1970 (Williams et al., 1970). Conductivity was 5.0 µS/cm in 1969, 6.56 µS/cm in 1984, but had increased markedly by 1987 to 31.6 µS/cm in the surface water. The ionic composition showed a dominance of $Na^+ > Ca^{2+} > Mg^{2+} >< K^+$ for the cations, and $HCO_3^- > Cl^- > SO_4^{2-}$ for the anions. This ionic dominance is a result of the geology of the catchment area and the contribution of ions through precipitation to the lake water (Balmaks, 1984). The pattern of ionic dominance in Blue Lake differs from the typical Australian pattern, where Cl^- is usually the predominant anion, and is different from those in the northern hemisphere where Na^+ is usually not dominant (Hart & McKelvie, 1986). Concentrations of phosphorus were low. The measured value of 0.012 ppm places the lake in the oligotrophic range of lakes, e.g. as compared to North Norwegian lakes (Aagaard, 1986). Aagaard (1986) recorded a total phosphorus maximum of 13 mg/m^3 in the oligotrophic Norwegian lakes. The nitrite and nitrate concentrations increased from 0.005 ppm in 1970 to 0.016 ppm in the surface water of Blue Lake in 1987. But the total nitrogen value of 0.15 ppm places Blue Lake in the ultra-oligotrophic range according to the measurements given by Aagaard (1986, 150 mg/m^3; for comparison see also White, 1983). The lake water was slightly acidic with the pH ranging from 6.0 to 6.6 which is a reflection of the acidity of the surrounding rocks and soils (Balmaks, 1984). Timms (1980c) gave some chemical characteristics of lake mud sampled at 26 m water depth in Blue Lake. Organic matter content was 12.1%, total Carbon 5.2%, Nitrogen 0.56%, and the C/N ratio 9.30.

9.2.6.4. Biological Features

The results of a zooplankton study by Bayly (1970) showed a plankton in Blue Lake mainly dominated by rotifers, with Asplanchna sp. the dominant species. Other rotifer genera present included Keratella, Polyarthra, and Monommata. Bayly also noted the occurrence of Chydoridae, i.e. Alona sp., Camptocercus sp., and Chydorus sp., as well as the copepod Eucyclops sp. In comparison, the zooplankton diversity in Lake Cootapatamba, one of the other three glacial lakes near Mt. Kosciusko, was greater. Benzie (1984) identified 11 taxa. The zooplankton in Lake Cootapatamba was dominated by Boeckella montana, B. pseudochelae, Daphnia nivalis, and in one month, Keratella slacki.

Phytoplankton were not recorded from Blue Lake apart from a small amount of the green filamentous Ulothrix (Powling 1970). The highest phytoplankton diversity was found in Lake Cootapatamba in the same study.

Timms (1980c) recorded 12 macrobenthic species from Blue Lake. The dominant species were Antipodrilus davidis (Oligochaeta), Chironomus oppositus (Diptera), and Glacipisium kosciusko (Mollusca). The results of Timms' study (1980c) indicated that the highest species numbers, abundance of organisms, and biomass were found in the sublittoral zone. Chironomid larvae (almost entirely C. oppositus) contributed 63% of the total mean biomass, followed by oligochaetes (25%). Besides C. oppositus, only two other chironomid species were recorded, Procladius sp. and Polypedilum nr. tonnoiri. Both the latter species had their highest abundances at water depths of 8 and 12 m. C. oppositus occurred in high abundances at each water depth sampled. Timms (1980c) suggested that allochthonous input was significant in Blue Lake. He commonly found decomposed leaves and twigs in his samples. These might be a major source of food for C. oppositus which is a surface-feeding detrivore.

The mountain minnow Galaxias findlayi is common in Blue Lake and it was suggested (Timms, 1980c) that the occurrence of fish in Blue Lake is the cause of the absence of the large planktonic cladoceran Daphnia nivalis. No fish were recorded from Lake Cootapatamba, where Daphnia nivalis was abundant (Benzie, 1984).

Ten taxa of Chironomidae were recorded from Blue Lake by the author (Table 9.2.). The profundal samples revealed the same species composition as was found by Timms (1980c). C. oppositus was the dominant species. It occurred in all samples and was most abundant in the sublittoral zone (6 and 9 m). Polypedilum was found only in the 6m sample, but Procladius occurred at most depths.

The remaining seven taxa were found mainly in hand-net samples collected in the littoral area of the lake, and the delta area of the main inlet on the western side of the lake. Paramerina levidensis and nr. Eukiefferiella (SRV sp. 38) were also found in the 6 m sample. These taxa are all new records for Blue Lake and all have been found as fossils in the core samples.

Larvae of three species of Trichoptera were found: Triplectides varius, Archaeophylas ochreus and an unidentified species of Philorheithridae.

The phytoplankton consisted only of Dinobryon, a characteristic form found in oligotrophic waters. The zooplankton was composed of copepod-nauplii and rotifers. Nearly the same species composition was found as that recorded by Bayly (1970), except for the new records of Euchlanis sp. and Notholca sp.

Table 9.2. Blue Lake : Biological Features on 3 March, 1987.
I. Chironomidae - the taxa present, their abundance (as individuals m^{-2}) with depth, and taxa found in littoral hand-net samples (P-present), * = new record for Blue Lake (NR).

Species/Depth	6m	9m	13m	15m	18m	20m	Hand-Net	NR
Chironomus ?oppositus	2198	1894	399	489	267	710	P	
Polypedilum sp.	44	0	0	0	0	0	-	
Tanytarsus sp.	44	0	0	0	0	0	P	*
Procladius sp.	0	45	0	44	0	67	P	
Paramerina levidensis	44	0	0	0	0	0	P	*
nr. Eukiefferiella sp.	44	0	0	0	0	0	P	*
E. claripennis gr.	0	0	0	0	0	0	P	*
Cricotopus sp. 12	0	0	0	0	0	0	P	*
Cricotopus sp.4	0	0	0	0	0	0	P	*
nr. Paralimnophyes	0	0	0	0	0	0	P	*

II. Qualitative Results: Trichoptera, Zooplankton, Phytoplankton.

Trichoptera [1] larvae in benthos and hand-net samples: Limnephilidae: Triplectides varius
Archaeophylas ochreus
Philorheithridae sp.

Zooplankton: Copepoda - nauplii,
Rotifera: Euchlanis sp., Polyarthra sp., Keratella sp., Notholca sp.,
Asplanchna sp.

Phytoplankton [2]: One colony of Chrysophyta was found: Dinobryon sp.

Identification was carried out by (1) Dr. R. St Clair, Zoology Dept., Monash University,
(2) P. Newall, Biol. Section, Rural Water Commission, Armidale, Australia.

9.2.7. Core Description and Dating of the Sediments

The 442 cm long core from Blue Lake was obtained on March 22, 1977 by Charles Barton (Bureau of Mineral Resources, Canberra), at a water depth of 24.5 m. The coring site in mid-lake was determined according to Barton's compass measurements (pers. com.). A pneumatic corer, similar to that designed by Mackereth (1958), was used. The sediment on the bottom of Blue Lake was too flocculent to carry the weight of the coring cylinder. Therefore, the corer sank into the sediment and approximately the first 50 cm of the sediment were lost. The core was labelled NA. In the field the plastic coring tube (diameter 5 cm) was cut in half vertically and rubber bungs were inserted in both ends of the coring tubes. Because of this procedure, 2-3 cm of the core were lost at the 223 cm horizon. In the laboratory the plastic tubes containing the sediment cores were split open and a core description was completed before the sampling of the core for microfossils, sediment, and radiocarbon analyses was carried out (see Chapter II). The core was then wrapped in aluminium foil and sealed in a plastic envelope. The core is kept in the Department of Geography and Environmental Sciences, Monash University, Clayton, Australia.

Two sediment layers of the core were radiocarbon-dated (Table 9.3.). The oldest organic deposits in the core revealed an age of 13,000 years. The layer between 39 and 42 cm was deposited 1700 years ago. For this study, finance was provided for only two radiocarbon dates. Therefore, some interpretations of the stratigraphy of the fossil chironomids from Blue Lake remain, for the time being, speculative with respect to dating. Some ages in the core under study were inferred from correlations of the NA core stratigraphies with the cores studied by Raine (1974). Three cores were taken by Raine (1974) at different sediment depths in the deepest part of the basin (26 m) and were subsequently treated as one composite core. The references in this study are to this composite core. In Appendix IV, Fig. 3.5 from Raine's thesis is reproduced with the permission of the author. This figure illustrates depth profiles of selected sediment fractions of the Blue Lake cores 1 and 3 (the composite core).

Table 9.3. Radiocarbon dates for sediment samples taken from the Blue Lake core.

Core Depth (cm)	Laboratory Number	Date
39-42	SUA 2600	1700 +/- 80 yr B.P.
407-409	SUA 2601	13,110 +/- 240 yr B.P.

The radiocarbon dating was carried out by the 'N.W.G. Macintosh Centre For Quaternary Dating', University of Sydney, N.S.W. Australia. The dates are conventional radiocarbon age. The results are the weighted mean of measurements in two counters.

The description of the stratigraphy of core NA is given in Fig. 9.2. The letter coding of the sediment zones is in agreement with sediment zones designated by Raine (1974, pp. 78, 81, 82). Core NA consisted mainly of homogenous brownish-black organic lake mud from the top of the core down to 332 cm. No laminations were visible. This zone correlated with zone A in Raine's composite core. A band reaching from 332 to 336 cm consisted of black organic mud with sand particles (zone B in Raine, 1974). The next layer, from 336 to 360 cm, was grey-black mud containing sand particles (zone C in Raine, 1974). At the 360 cm horizon a change of colour from grey black to a medium olive grey mud occurred (zone D in Raine, 1974). This layer reached to 388cm. Between 388 and 400 cm, the mud was uniformly dark grey (zone E in Raine, 1974). A lamination occurred between 400 and 402 cm of the core. The colour of this lamination was a light grey and the mud contained sand particles (zone F in Raine, 1974). The next layer of sediments (402-408 cm) was dark grey mud, representing the oldest organic deposits in the lake (zone G in Raine, 1974). A sharp change occurred at the 409 cm horizon; the colour of the sediments changed to light to medium grey and the sediments consisted of clay and silt with an increasing amount of fine sand towards the bottom of the core.

Because the sediment zones of the cores analysed in the two studies could be correlated, it was possible to infer some dates for the NA core from the radiocarbon dating carried out in Raine's study (1974). The oldest organic sediments were dated as 13,000 yr B.P. Zone F was deposited approximately 12,000 yr B.P., the border between zone E and D represented 11,000 yr B.P., the top of zone D was dated 10,000 yr B.P., and the top of zone C was dated as being 9000 yr B.P.

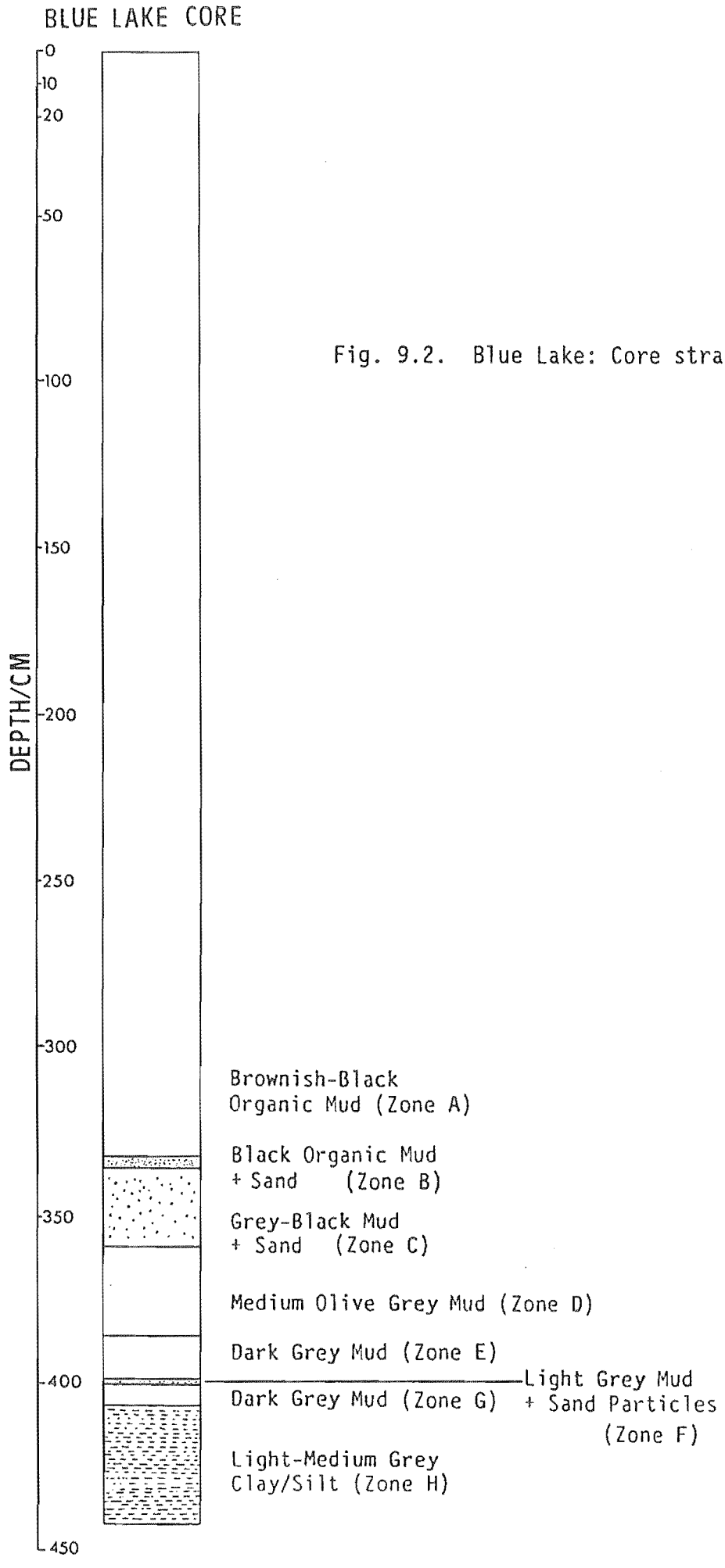


Fig. 9.2. Blue Lake: Core stratigraphy.

With only two radiocarbon dates, it was not possible to determine the sedimentation rate in core NA. According to Raine (1974), the sedimentation rate in the cores from Blue Lake declined from a time before 13,000 yr B.P. until about 9000 yr B.P., in line with a decreasing proportion of coarse material in the sediment. After 9000 yr B.P. the sedimentation rate rose abruptly, reaching a peak between 8000 and 7000 yr B.P. The sediment deposited at this time contained a higher percentage of detritus herbosus. The sedimentation rate was at a minimum at about 6000 yr B.P., after which it rose to recent levels.

9.2.7.1. Water Content and Loss-on-Ignition

The results of the determination of water-content and loss-on-ignition for 25 sediment samples from the Blue Lake core are shown in Fig. 9.3. The samples for the sediment analysis were taken parallel to samples collected for microfossil analysis. The sediment samples were taken mainly at 20 cm intervals, but closer sampling intervals were chosen at levels in the core which exhibited lithological changes.
The water content in the samples varied between 16.5% in the oldest sediments to 83.5% in the 10 cm sample. From the low value at the bottom of the core (clay/silt), the water content increased considerably at the 408 cm horizon to 44.3% when the sediments changed to dark grey mud. After a slight drop at the 403 cm level, the water content increased steadily to 81.0% in the 221 cm sample and remained at this level throughout the rest of the core.

Loss-on-ignition was correlated throughout the core with the water content profile. Values ranged from 2.9% of dry weight of sediment to 33.2% in the 221 cm sample. Very low concentrations at the bottom of the core increased to 13.5% at the 363 cm level, then to 23.4% in the following sample, remained stable in the layer between 338 and 303 cm, and increased again to nearly 30% at the 283 cm horizon. In the sediments between 263 and 120 cm, the organic matter content remained relatively stable, fluctuating around 30%. At the 100 cm horizon, the organic matter content dropped to 26.4%, and was generally lower in the younger sediments up to the top of the core.

Blue Lake

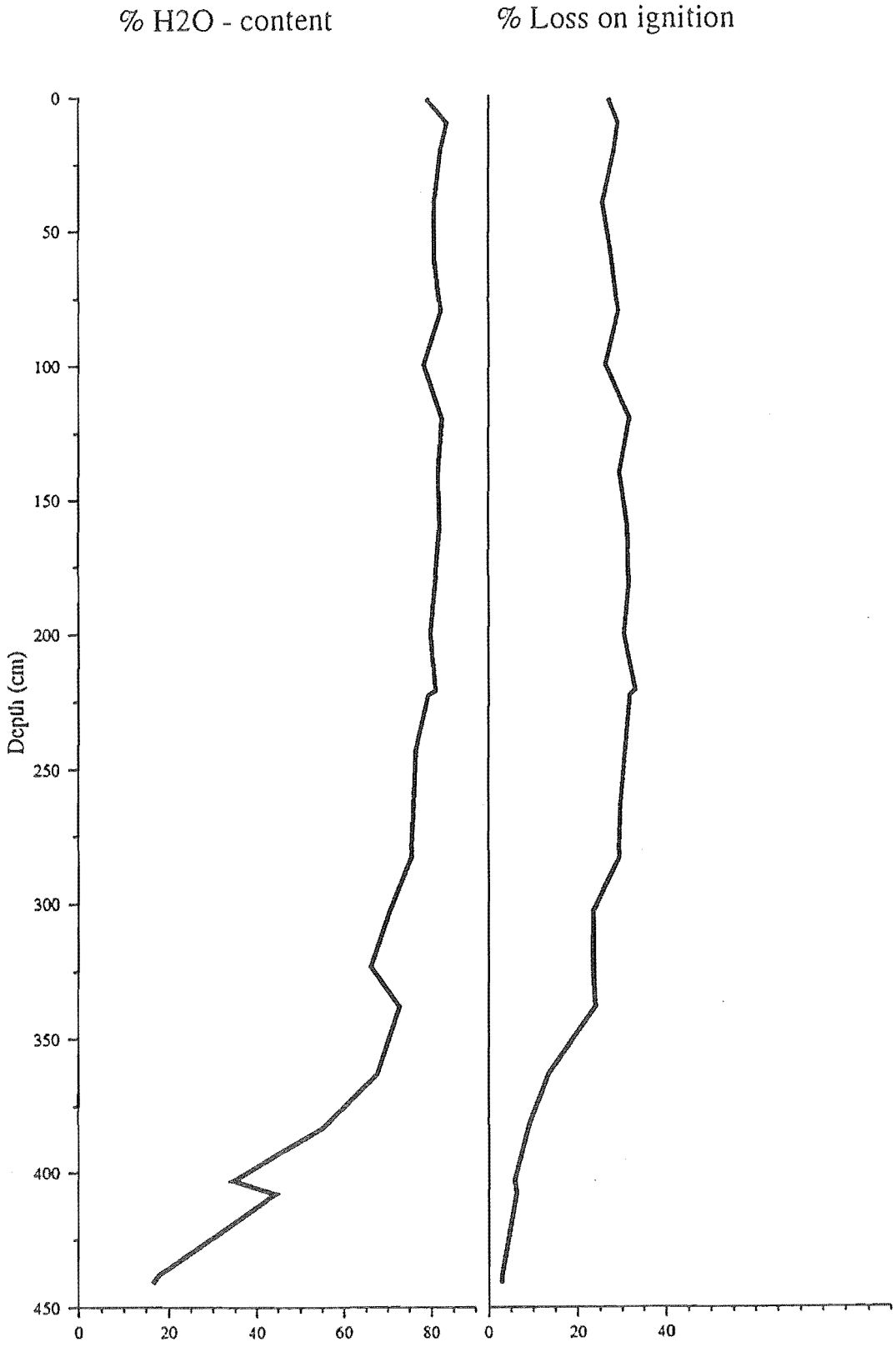


Fig. 9.3. Profiles of water content (as % of wet weight) and loss-on-ignition (as % of dry weight) in the sediment core from Blue Lake.

9.2.7.2. A qualitative account of the fossil Cladocera from Blue Lake

During the chironomid counts on the quantitative microscope slides, remains of fossil Cladocera were noted and identified but not as yet counted. Cladocera remains were rare in the Late-Pleistocene samples, but became abundant in all samples derived from sediment-zone A representing the Holocene. Nearly all fossils encountered belonged to the benthic Chydoridae. No Daphnia ephippia were found, but some head shields of Bosmina occurred exclusively in the 120 cm sample. The following species of Chydoridae were recognized: Camptocercus australis, Alona pulchella, Alona quadrangularis, Alona cf. rectangula, Biapertura affinis, and Biapertura setigera. Two taxa could be identified only to generic level: Chydorus sp. and Pleuroxus sp.

9.2.8. Taxonomy of the Chironomid Taxa found in this Study

The following section contains a brief description of the main morphological characteristics of the fossil and recent chironomid taxa from Blue Lake on which the distinction of the taxa was based. Most taxa could only be identified to generic level. Several as yet undescribed taxa were found. Photomicrographs of the head caspules of most taxa are presented in Appendix I (Fig. I - III), and are referred to in the text.

Orthocladiinae

This group presented the most difficulties for identification of the present-day larvae and the fossil material. In the fossil fauna, sixteen taxa could be distinguished and of these, five taxa could be placed generically. The morphological features of the following taxa are similar to those in the South Island material and are not described here (see Chapter IV, section 4.1.): Orthocladiinae sp. I (Fig. II-O), Orthocladiinae sp. V (Fig. III-T), Orthocladiinae sp. XIV (Fig. II-M), Eukiefferiella claripennis gr. (Fig. II-N), and Corynoneura sp. (Fig. III-S). As there are two described species of Corynoneura in Australia (Cranston & Martin, 1989), it was not possible to identify these head capsules beyond generic level.

V. Pettigrove, Rural Water Commission, Armidale, Australia, has worked extensively with the Australian Cricotopus/Orthocladius complex. Using his key (Pettigrove, unpubl.) three species of Cricotopus could be distinguished in the fossil fauna from Blue Lake.

All three Cricotopus taxa from Blue Lake have one median tooth and six pairs of lateral teeth. Cricotopus sp. 12 can be separated from the other taxa by the uneven outline of the mentum, a consequence of the reduction in size of the second pair of lateral teeth; by the darkened premandibles; and by the crenulation of the inner sides of the mandibles. Cricotopus sp. 4 has a mentum from which the median and first pair of lateral teeth project forward, and its mandibles are heavily crenulated at the outer margin. In head capsules of Cricotopus annuliventris gr., neither margin of the mandibles is crenulated and the mentum is even in outline.

The taxon nr. Eukiefferiella sp. SRV 38 (Fig. III-R) was found as fossils in the core and two living larvae were obtained from the littoral zone of Blue Lake (see 9.2.6.4.). Dr. Peter Cranston (ANIC, Canberra) now refers to this taxon as 'grape th' SRV sp. 38, as the pupa has conspicuous thoracic horns that look like a bunch of grapes (pers. comm.).

The larva from Blue Lake is small, 4.5 mm long. The anterior and posterior parapods are separated, each bearing an apical crown of claws. Procerci are present, each bearing seven anal setae. The head capsule has a mentum, which resembles that of Eukiefferiella. It is composed of two median teeth that are taller than the lateral teeth, and five pairs of lateral teeth. The sclerotization below the mental teeth appears striated through the alternation of darker and lighter longitudinal bands. Ventromental plates are present with well-developed beards (in this morphological feature nr. Eukiefferiella differs from Eukiefferiella). The mandible has an apical tooth, which is shorter than one half of the combined width of the four inner teeth. The seta subdentalis is lancet-like, the seta interna is composed of five plumose branches. There appears to be an additional tooth below the apical tooth on the inside of the mandible. The mola is without spines, which is in contrast to Eukiefferiella larvae whose molae carry one to five spines. All setae on the labrum are simple,

the pecten epipharyngis is composed of three pointed narrow scales. The premandible has one broad apical tooth and one pointed inner tooth. The brush is absent. The antenna is five-segmented, with all segments being sub-equal in size. The exception is segment four, which is nearly as long as segment three. The antennal blade possesses one accessory blade and extends to about one half of the terminal segment. The ring organ is in the basal third of the first antennal segment. The Lauterborn organs extend as high as the third antennal segment.

Nr. Paralimnophyes was found as fossils in the core and one living larva was collected from the littoral of Blue Lake (see 9.2.6.4.). The larva keyed to Paralimnophyes in Wiederholm (1983), but differed in several characters, e.g. the larva from Blue Lake does not possess long setae on the body segments. SI (setae anteriores) is also different in that it is simple but with an accessory tooth.

The larva from Blue Lake is small, about 4 mm long. The body is coloured a darkish mottled brown. Procerci are present, two thirds as wide as they are long, bearing seven anal setae. Anterior and posterior parapods are divided, each bearing a crown of claws. All claws on the posterior parapods are simple. The head capsule is a darkish brown with a well-developed post-occipital margin and heavily sclerotized. The mentum possesses paired median teeth, taller than the first of five pairs of lateral teeth. A tooth is present at the base of the mentum. The labrum has simple setae, except SI, which bears an accessory tooth. The pecten epipharyngis consists of three pointed scales with five chaetulae laterales on each side. The pair nearest to the pecten epipharyngis is broad, whereas the remaining chaetulae lateralis are narrow. The premandible has two apical teeth and two inner teeth, the brush is apparently absent. The mandible has an apical tooth, which is shorter than the combined width of the four inner teeth. The seta subdentalis is short and pointed and the seta interna has five setae becoming plumose apically. The antenna has a length of two-thirds of the mandible length, and is five-segmented with segment four being three times as long as segment three. The blade extends beyond the apical segment. The Lauterborn organs are distinct.

The following taxa have been found as fossils in the core only. The distinction between the taxa is based mainly on the menti of the head capsules.

Head capsules of Orthocladiinae sp. III (Fig. III-Q) can be separated from the other taxa by the weakly sclerotized mentum possessing two rounded median teeth distinctly separated by a groove one half the width of one median tooth, and five pairs of lateral teeth, which diminish in size laterally. Ventromental plates are absent. The mandibles are highly arched with one apical tooth and three inner teeth. The length of the apical tooth is about one half of the combined width of the inner teeth. The premandible appears to have one broad apical tooth.

Orthocladiinae sp. IV (Fig. II-P) head capsules have a very characteristic mentum with one broad median tooth and four pairs of lateral teeth. The median tooth is as wide as the combined width of the first pair of laterals. It is flat with a small point about the middle of the tooth and is slightly less sclerotized than the lateral teeth with sclerotized longitudinal grooves appearing as striations below it. The first pair of laterals protrude above the height of the median tooth. Ventromental plates are present.

Fossils of Orthocladiinae sp. X (Fig. II-J) have a mentum with two rounded distinctly separated median teeth, which are as wide as the combined width of one side of the lateral teeth, and five pairs of lateral teeth diminishing in size laterally. The median and first pair of lateral teeth are slightly less sclerotized than the remaining lateral teeth and have sclerotized longitudinal grooves appearing as striations below them. Ventromental plates are present with well-developed beards. The mandibles have one apical tooth, which is shorter than the combined width of the four inner teeth.

The mentum of Orthocladiinae sp. XII (Fig. II-K,L) has two median teeth and six pairs of lateral teeth. The median teeth protrude forward, the first pair of laterals are reduced in size so that the second pair of lateral teeth reaches higher than the first pair. The remaining four pairs of lateral teeth are very much smaller than the second pair and diminishing in size laterally.

The fossil head capsules of Orthocladiinae sp. XIII (Fig. II-I) are characterized by a mentum with one median tooth displaying lateral notching and five pairs of lateral teeth. The median tooth and the first pair of laterals protrude well above the remaining four pairs of lateral teeth, which diminish in size laterally. Longitudinal sclerotized grooves appear below the median tooth. Ventromental plates are present.

Head capsules of Prodiamesinae (?) (Fig. I-H) possess unusual menti. This taxon might belong to the Orthocladiinae because Prodiamesinae are not yet described from Australia, but the head capsules of this taxon exhibit the large ventromental plates, extending far beyond the outer mental teeth, which are typical for the Prodiamesinae. The mentum of the head capsule has one broad median tooth, which is wider than the combined width of the first pair of lateral teeth, and which is pointed distinctively. The first pair of laterals are lower than the median tooth, and the second pair of laterals reaches nearly as high as the first pair. There are all together six pairs of lateral teeth. The median tooth and the first pair of laterals are less sclerotized than the other lateral teeth.

Podonominae

Head capsules belonging to the Podonominae could be separated into Parochlus (Fig. I-G) and Podonomus (Fig. I-F). Distinguishing features of the two types of head capsules have been described in Chapter IV (Section 4.1.). Although several species of both genera have been described from New Zealand, on mainland Australia only one species is described in each genus, Parochlus tonnoiri and Podonomus collesi (Cranston & Martin, 1989). Because larval characteristics are not sufficient for species identification, it was not possible to positively associate the fossil Podonominae head capsules with the described species.

Chironomini

Five Chironomini taxa were recorded from Blue Lake, some of them as fossils and living larvae. The identification of most of the taxa did not present any difficulties. One undescribed taxon occurred in the fossil material, Chironomini sp. A (Fig. I-A), whose morphological features resemble Chironomini sp. A from New Zealand (see Chapter IV, Section 4.1.). As might be the case with this taxon from New Zealand, the Australian Chironomini sp. A might be the larvula of Chironomus.

Living larvae of Chironomus from Blue Lake (see 9.2.6.4.) were identified cytologically by Dr J. Martin, Melbourne University, as belonging to the Chironomus oppositus gr. so that most probably the fossil head capsules belong to this species as well.

Some of the morphological features of Riethia (Fig. I-B) have already been described in Chapter IV, Section 4.1. There are four described species of this genus in Australia (Cranston & Martin, 1989) so that it was not possible to identify this taxon to species level.

Timms (1980) found larvae of Polypedilum in benthic samples from Blue Lake which were identified as Polypedilum nr. tonnoiri. The larvae found by the author on March 3, 1987, do not key to P. tonnoiri in Martin's key to the Australian larvae of Polypedilum (unpubl.). The third antennal segment is not reduced in the larvae found by the author but is slightly longer than one third of the second segment. The ventromental plates are slightly more than twice as long as wide. These morphological characters key the larvae out to P. oresitrophum, a species which is recorded from New South Wales amongst other species of this genus (Cranston & Martin, 1989). The antennae were missing in all fossil head capsules of Polypedilum so that it was not possible to associate the fossils with either species.

The fossil head capsules of Xenochironomus (Fig. I-C) possibly belong to Xenochironomus canterburyensis, which is the only described species in Australia (Cranston & Martin, 1989).

Tanytarsini

In the Tanytarsini, only two taxa could be distinguished. Tanytarsus sp. (Fig. I-D, in Fig. 9.5. named Tanytarsini sp. 1 because the figure was drawn before positive identification) was found as living larvae in the littoral samples from Blue Lake and as fossils in the sediment core. Tanytarsus van der Wulp represents one of the largest chironomid genera in Australia with 26 described species (Cranston & Martin, 1989). It was not possible to identify the fossil head capsules or the living larvae to species level.

Tanytarsini sp. I (Fig. I-E in Appendix I; in Fig. 9.5. named Tanytarsini sp. 2) can be separated from Tanytarsus by the relatively strongly arched mentum with a rounded median tooth with slight notches laterally, by the arched ventromental plates, which are almost in contact medially and are about 4x as long as wide, and by the striations on the ventromental plates, which covers only the median region of the plate. The premandible is bifid, and the pecten epipharyngis is composed of three serrated scales.

Tanypodinae

Three Tanypodinae taxa occurred as fossils in the core and two of those were also found as larvae on March 3, 1987 (see 9.2.6.4.). The larvae of Procladius from Blue Lake have a concave ligula, and the smaller claws of the posterior prolegs are high-arched with points on the inner edge. With these morphological features they key to Procladius martini in Martin's unpublished key to the Australian Tanypodinae larvae.

Larvae of Paramerina from Blue Lake were reared to adults and identified as Paramerina levidensis (Fig. III-V). Fossil head capsules were positively associated with this species.

Tanypodinae sp. I (Fig. III-U) exhibits similar features to Tanypodinae sp. I from New Zealand (see Chapter IV, Section 4.1.) except for the length of the first antennal segment. Whereas the first antennal segment in the New Zealand fossils is relatively short

(nearly the length of the mandible), the first antennal segment in the Blue Lake fossils is longer then one half of the head capsule length. Larvae of Paramerina also have long first antennal segments so that these fossils from Blue Lake might be the second instar larvae of Paramerina, whereas in New Zealand, Tanypodinae sp. I might be the second instar larva of Apsectrotanypus.

9.3. Results

For the analysis of fossil chironomids, 39 samples consisting of 1 ml of wet sediment from the Blue Lake core were processed according to the methods described in Chapter II. All remains found in the sediment samples were counted. Three samples taken from the oldest sediments of the core (437, 417 and 412 cm) did not contain any chironomid head capsules. These samples were obtained from sediment zone H, the basal clay and silt layer of the core. The first chironomid fossils appeared at the base of zone G at the 407 cm horizon (for sediment zones see Fig. 9.2.).

The remaining 36 samples contained 2399 chironomid head capsules with an average of 66.6 head capsules per ml of wet sediment. The lowest number of remains (6) was found at the 402 cm level in the core (zone F), whereas the highest number of 188 head capsules occurred in the 352 cm sample (see Appendix, Table IV.2.).

The occurrence of chironomids in the oldest sediments of the core (above zone H) was low (Fig. 9.4.) but increased steadily to a maximum at 352 cm, except for the temporary decline of fossil numbers to the minimum occurrence of chironomid remains in the 402 cm sample. Above the 352 cm horizon, the number of remains declined again. The 342 cm sample contained only 79 head capsules. The chironomid abundance increased in the following sediment layers to reach a second maximum between 322 and 302 cm in the core. The numbers of head capsules decreased in the sediments above the 302 cm horizon and remained relatively stable showing only minor fluctuations up to the top of the core. The exception is a single peak abundance of 148 head capsules at the 221 cm horizon.

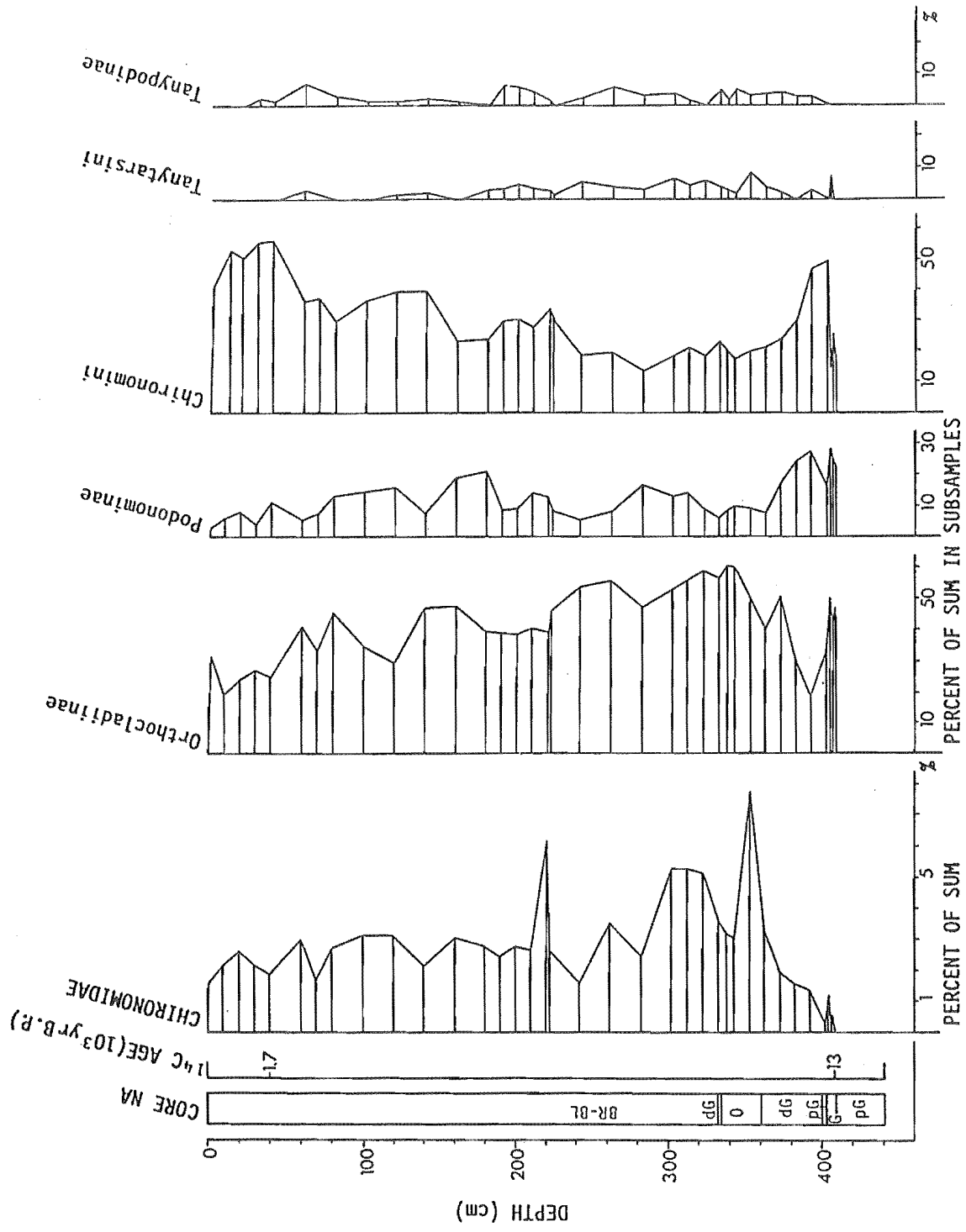


Fig. 9.4. Distribution of fossil chironomid head capsules (% of total fossil sum), and the relative abundance (% of number of head capsules at each sample level) of the chironomid subgroups in the core from Blue Lake. The core lithography and radiocarbon dates for two sediment horizons are given in column one and two. The letters used stand for: BR-BL: Brownish-Black, G: Grey, O: Olive Grey, P: pale, d: dark.

The fossil material from the Blue Lake core could be separated into five chironomid subgroups (Table 9.4.). Orthocladiinae were the most important subfamily with 44.3% relative abundance, followed by the Chironomini with 29.4%. Podonominae occurred with a relatively high abundance of 11.4%, whereas Tanytarsini made up only 3.1% of the fossil material and Tanypodinae were found with a relative abundance of only 2.5%.

The distribution of the chironomid subgroups (Fig. 9.4.) showed that remains of only three sub-groups of chironomids occurred continously in every sample of the core. These sub-groups are the Orthocladiinae, Chironomini, and Podonominae. Orthocladiinae were the dominant chironomids in most samples in the older sediments between 407 and 140 cm. The relative abundance of Orthocladiinae declined temporarily in two samples (402 and 392 cm), in which Orthocladiinae were sub-dominant. At 120 cm, in the more recent sediments, the composition of the chironomid fauna began to change. The relative abundance of Orthocladiinae declined and remained relatively low in the following sediment layers up to the top of the core.

The distribution of Chironomini in the core showed a maximum of abundance in the older sediments of the core at the 402 to 392 cm horizon after initially relatively low relative abundances in the oldest fossil-bearing sediments. Above the 392 cm level the Chironomini abundance declined and remained low and relatively stable up to the 140 cm horizon. A slight peak in abundance occurred at the 223 cm horizon. In the younger sediments (above 140 cm) Chironomini became the dominant component of the fossil chironomid fauna. The highest abundance of Chironomini was found in the youngest sediments.

Podonominae were important throughout the core. Their relative abundance showed a maximum in the older sediments of the core up to the 392 cm horizon. Above that level the distribution of Podonominae remained relatively stable but their relative abundance was generally lower in the youngest sediments.

Tanytarsini and Tanypodinae occurred in low relative abundances in the core. Neither Tanytarsini nor Tanypodinae head capsules were found in the oldest deposits. The first Tanytarsini remains were found at the

402 cm horizon and this sub-group had slightly higher relative abundances in the older sediments. The numbers of Tanytarsini decreased in the younger part of the core. Tanypodinae did not colonize the lake at the beginning of its existence. Their head capsules appeared first at 392 cm, occurred then in most of the following samples in very low relative abundances and disappeared in the top sediments of the core (above 30 cm).

A total of 28 chironomid taxa was distinguished (Table 9.4.) in the core. Of those taxa only 16 taxa occurred with a relative abundance of more than, or equal to, 1% of the total fossils. The highest species diversity was found in the Orthocladiinae with 16 taxa. The highest number of undescribed taxa (11 taxa) was also found in the Orthocladiinae although two of those taxa could be placed near a described genus (see section 9.2.8.). Only eight Orthocladiinae taxa occurred with a relative abundance of more than, or equal to, 1% of the total fossils. These were: nr. Eukiefferiella sp. SRV 38, Cricotopus sp. 12, Eukiefferiella claripennis gr., Orthocladiinae sp. I, nr. Paralimnophyes sp., Corynoneura sp., Orthocladiinae sp. III, and Cricotopus sp. 4. Five Chironomini taxa occurred (including one undescribed taxon), four of which accounted for more than 1% of the total fossils: Chironomus oppositus gr., Chironomini sp. A, Polypedilum sp., and Riethia sp. Two taxa were found in the Tanytarsini (Tanytarsus sp. and Tanytarsini sp. I) and Podonominae (Podonomus and Parochlus) all of which occurred with more than 1% of the total fossils. Tanypodinae head capsules could be differentiated into three taxa with one of those being undescribed. All Tanypodinae taxa were found in percentages lower than 1% of the total fossils.

The number of taxa found in the samples of the core ranged from the four taxa in the 402 cm sample to the maximum of 22 taxa in the 352 cm sample. In the oldest fossil-bearing sediments of the core, which were deposited during the Pleistocene (407-360 cm), the number of taxa was generally low but increased from 5 taxa in the 407 cm sample to 13 in the 362 cm sample (see Appendix, Table IV.2.). In the samples from the Holocene, the number of taxa found varied between 12 and 22 taxa in the sediments between 352 and 60 cm. Numbers of taxa in the samples were generally higher in the older part of the Holocene. In the youngest sediments (40 cm to the top of the core), the number of

Table 9.4. Blue Lake: Fossil Chironomid Taxa (N - total numbers found in all samples, % - relative abundance in percent of the total number).

TAXON	N	%
nr. *Eukiefferiella*	465	19.4
Cricotopus/Orthocladius sp. 12	138	5.8
Eukiefferiella claripennis gr.	99	4.1
Orthocladiinae sp. I	87	3.6
nr. *Paralimnophyes*	58	2.4
Corynoneura	56	2.3
Orthocladiinae sp. III	42	1.8
Cricotopus/Orthocladius sp. 4	24	1.0
Cricotopus annuliventris gr.	14	0.6
Orthocladiinae sp. IV	12	0.5
Orthocladiinae sp. X	12	0.5
Orthocladiinae sp. 14	7	0.3
Orthocladiinae sp. XIII	6	0.3
Orthocladiinae sp. V	5	0.2
Orthocladiinae/Prodiamesinae (?)	3	0.1
Orthocladiinae sp. XII	2	0.1
Chironomus oppositus gr.	472	19.7
Chironomini sp. A	135	5.6
Polypedilum	55	2.3
Riethia	44	1.8
Xenochironomus	5	0.2
Tanytarsus	45	1.9
Tanytarsini sp. I	27	1.1
Podonomus	148	6.2
Parochlus	110	4.6
Procladius	22	0.9
Paramerina levidensis (Skuse, 1889)	17	0.7
Tanypodinae sp. I	9	0.4
Orthocladiinae	1057	44.1
Chironomini	711	29.6
Tanytarsini	74	3.1
Podonominae	273	11.4
Tanypodinae	61	2.5
not ident.	223	9.3
ident. only to subfamily	57	2.4

chironomid taxa declined again and ranged from 8 taxa in the top sample to 11 taxa in the 20 cm sample.

In Fig. 9.5. the stratigraphy of the most abundant chironomid taxa is given. Nr. Eukiefferiella in this graph denotes the stratigraphy of nr. Eukiefferiella sp. SRV 38, Eukiefferiella sp. is E. claripennis, and Orthocladiinae sp. VII is nr. Paralimnophyes (Table 9.4.). The latter name change is due to the drawing of the figure before positive identification. The distribution of the most abundant fossil chironomid taxa through time indicates that two taxa dominated the fossil chironomid fauna during most of the lake's past. These were Chironomus oppositus (19.7%) and nr. Eukiefferiella sp. SRV 38 (19.4%).

Nr. Eukiefferiella appeared with a low relative abundance in the 406 cm sample. In the oldest fossil bearing sediments the relative abundance fluctuated strongly reaching the maximum abundance of this taxon in the core at the 342 cm horizon. Above that sediment level, nr. Eukiefferiella was the dominant taxon in the fauna up to the 223 cm level. In most samples up to the top of the core, nr. Eukiefferiella remained the subdominant taxon, except for the minimum abundance at the 30 cm level.

Of the other Orthocladiinae taxa, Orthocladiinae sp. I and Cricotopus sp.12 had higher abundances in the lower half of the core. Cricotopus sp. 12 had a single peak abundance at the base of zone G. The relative abundance of Cricotopus sp. 4 was very low throughout the core, except for a slight maximum in the oldest sediments of the core. The distribution of nr. Paralimnophyes in the core showed maximum occurrence in the 406 cm sample. Above that horizon the relative abundance of the taxon declined and remained low in the older part of the core. This taxon was then slightly more abundant in the upper part of the core. The relative abundance of E. claripennis fluctuated throughout the core. Generally lower abundances were found in the oldest part of the core and in the younger sediments above the 120 cm level. Corynoneura occurred in low relative abundances which remained more or less stable throughout the core. The distribution of one orthoclad taxon, Orthocladiinae sp. III, although present with a

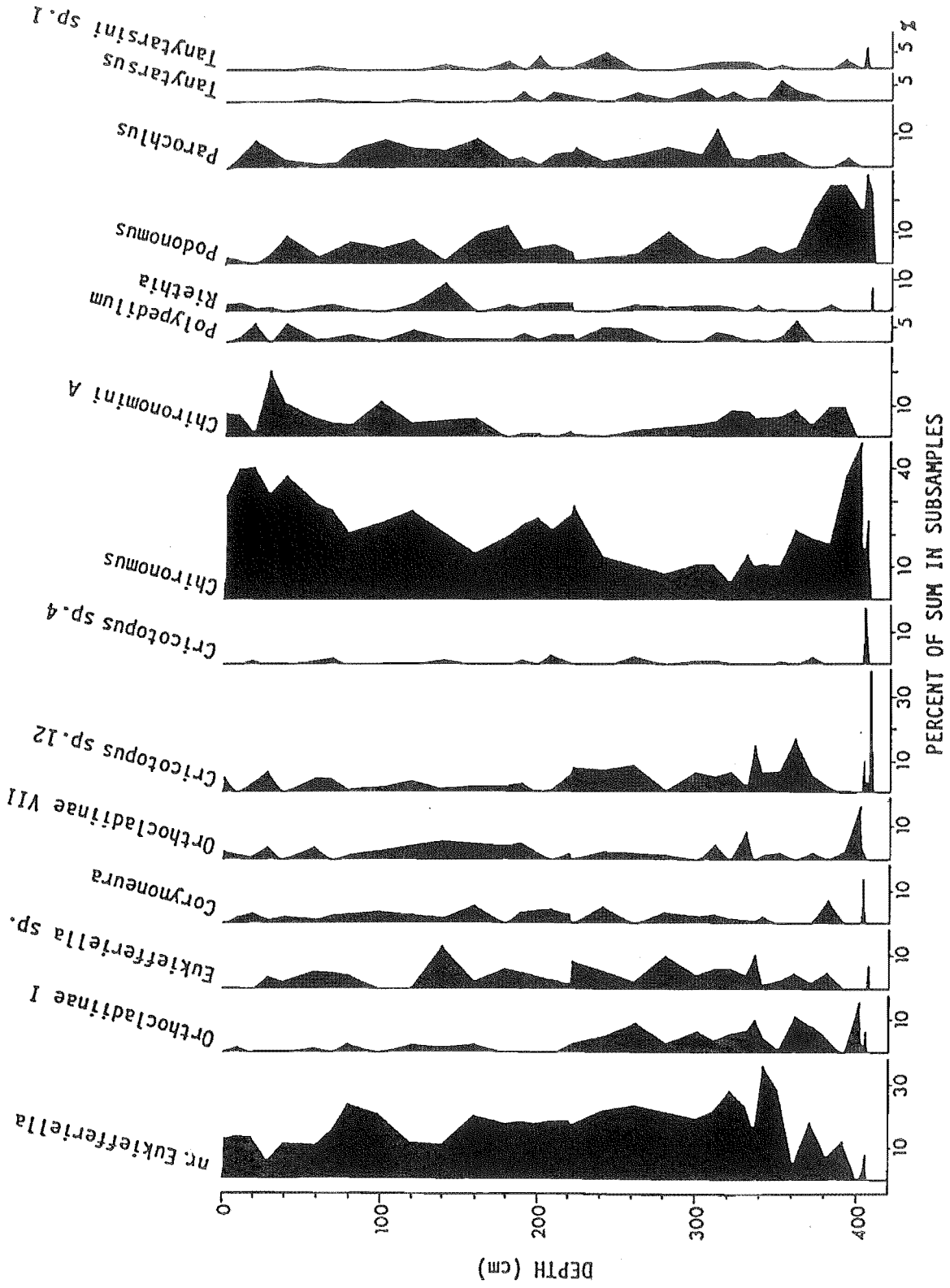


Fig. 9.5. Blue Lake: Relative abundance (as percent of the fossil sum in the samples) of selected chironomid taxa in the core.

relative abundance of more than 1%, has not been displayed graphically. This taxon had a similar stratigraphy to Orthocladiinae sp. I. It was generally more abundant in the older sediments in the core and disappeared entirely above the 80 cm horizon (see Appendix, Table IV.3.)

Chironomus appeared in a low abundance in the 407 cm sample. The relative abundance of this taxon increased in the following samples to reach a pronounced maximum at the 404 cm level and then decreased in the following sediment layers to the minimum occurrence in the 322 cm sample. The relative abundance of Chironomus remained low in the next samples but increased at the 221 cm horizon showing only minor fluctuations in the above sediments, and increased again in the youngest sediments, when Chironomus became the dominant chironomid in the fossil fauna.

Chironomini A was found in most samples of the core. This taxon had two maxima of abundance, in the older sediments of the core and in the more recent sediments. Polypedilum did not colonize the lake at the beginning of its lacustrine phase. This taxon occurred first in the 362 cm sample and was found in most samples of the core in low relative abundances. The relative abundance of Riethia fluctuated only slightly in the core. The highest abundance of this taxon was found at the 140 cm level.

The two Tanytarsini taxa were more abundant in the lower half of the core. Tanytarsus did not occur until the 372 cm horizon. Both taxa disappeared entirely above the 60 cm horizon.

Parochlus was found only in two samples in low abundances in the oldest sediments of the core, but above the 352 cm level occurred in most samples in the core with a relatively stable abundance. Podonomus constituted the third important fossil chironomid in the core with a relative abundance of 6.2% of the total fossils. This taxon had its maximum occurrence in the oldest sediments in the core, in which it was either the dominant (404, 382 cm) or the subdominant (407, 406, 402, 392, 372 cm) chironomid of the fossil fauna. Above the 362 cm horizon the relative abundances of Podonomus declined and remained relatively stable throughout most of the core with slight

maxima at the 282 and 180 cm levels. The lowest relative abundances of Podonomus were found in the youngest sediments.

To summarize, 28 chironomid taxa were distinguished in the fossil chironomid fauna from Blue Lake. The fauna was dominated by three taxa, Chironomus, nr. Eukiefferiella, and to a lesser extent by Podonomus. The maxima of these three taxa occurred during different periods of the lake's history during the last 13,000 years.

9.3.1. Numerical Analyses

The temporal community structure of the fossil chironomid fauna in the core from Blue Lake was examined using a classification analysis and an ordination technique (correspondence analysis) (see Chapter II). The data matrix for the data analyses consisted of the percentage abundance of 16 chironomid species (those with a relative abundance of =/>1%) in 36 samples. The three samples from the basal clay/silt layer of the core were omitted from the analyses because they contained no chironomid head capsules.

The hierarchical cluster analysis (see Chapter II) performed to study species associations used the percentage similarity of community (PSc)-index and group average clustering (Fig. 9.6.).

Three distinct and homogenous groups of sediment sequences were distinguished by the cluster analysis, whereas seven of the oldest samples were classified as outliers (Fig. 9.6., the sample code is given in Table IV.3 in the Appendix). The groups formed consisted of the following sediment sequences:

Group I: samples 33 - 36 (40 cm to the top of the core), and one sample from the oldest sediments, sample 5 (392 cm).
Group II: samples 19 - 31 (223 - 60 cm),
and one sample from Group III, sample 16 (282 cm).
Group III: samples 9 - 18 (352 - 242 cm).

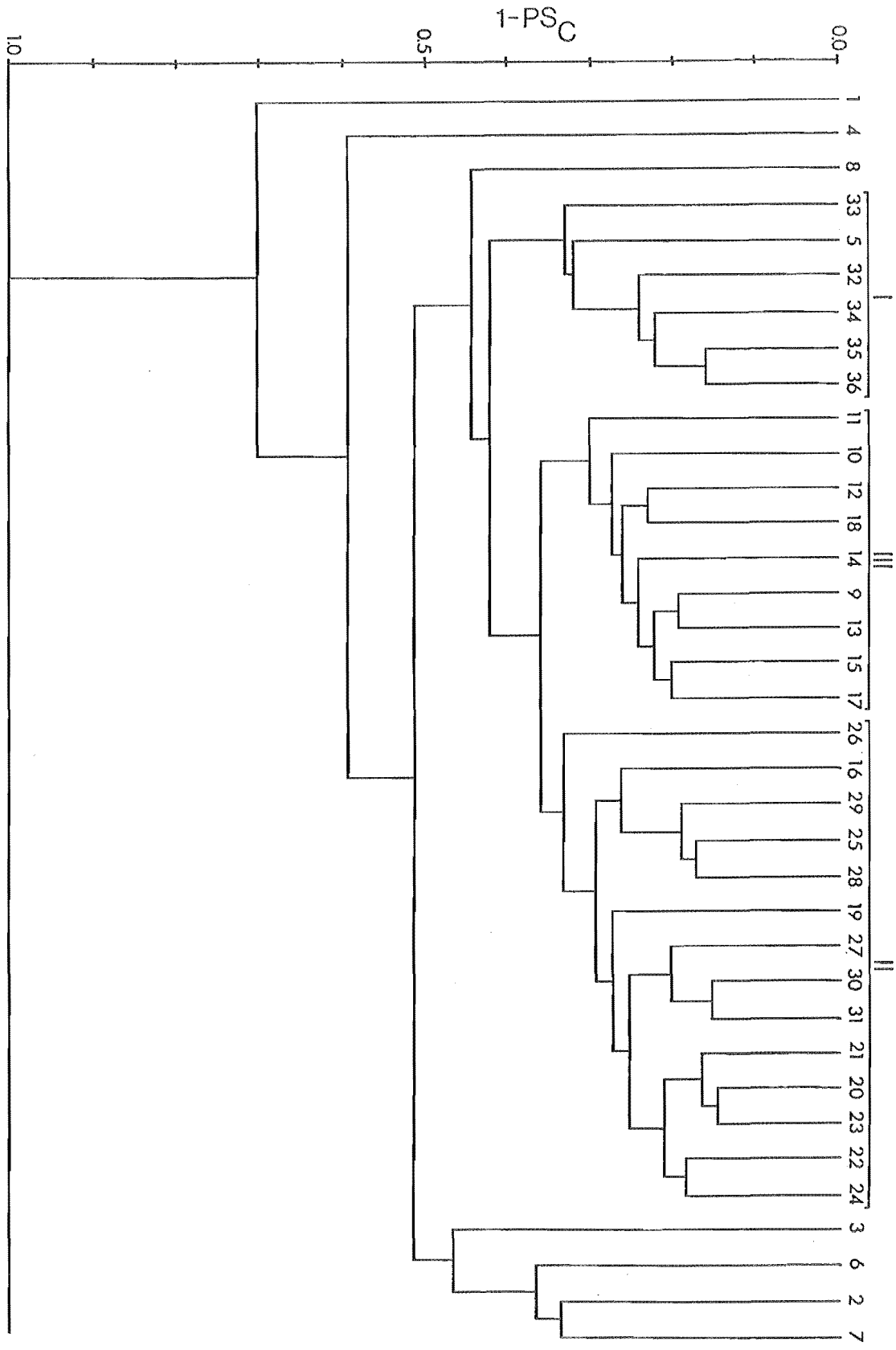


Fig. 9.6. Dendrogram based on an average linkage cluster analysis on the relative abundance of fossil chironomid taxa in the core. The vertical axis gives the values of the dissimilarity index. The group codes are indicated by Roman numerals.

The results of the classification analysis indicate vertical changes in the composition of the fossil chironomid fauna in the core following the time series of the samples during the Holocene. All samples deposited during the Holocene (352-1 cm) were placed in one of the three groups of sediment sequences (only one of the samples deposited during the Late-Pleistocene, sample 5=392 cm, was placed with the Holocene samples). Group I represents the youngest sediments deposited ca. 1700 yr B.P. and later (Fig. 9.4.), Group II represents the intermediate period and Group III the oldest period of the Holocene (dating inferred from Raine, 1974).

In Table 9.5., the mean relative abundances of the chironomid species in each group are shown for the three clusters. Group III was characterized by the dominance of nr. Eukiefferiella and the lowest relative abundance of Chironomus; Group II had relatively high abundances of nr. Eukiefferiella and Chironomus; and Group I was characterized by a chironomid fauna dominated by Chironomus, a very low occurrence of nr. Eukiefferiella, and the absence of Tanytarsini.

In addition to the temporal dominance pattern of the fauna, several other trends in community structure can be observed. Samples in Group I showed, besides the dominance of Chironomus, the highest relative abundances of nearly all Chironomini taxa (except for Riethia), whereas the relative abundances of most Orthocladiinae taxa were at their lowest values with the exception of that of nr. Paralimnophyes. These trends were reversed in the samples of Group III, in which most Chironomini taxa had their minimum occurrences and Orthocladiinae taxa occurred with their maximum relative abundances. Both Tanytarsini taxa had their highest relative abundances in Group III, whereas of the two Podonominae taxa, Podonomus occurred with its lowest relative abundance in Group III, and Parochlus had its minimum occurrence in Group I. Samples of Group II showed intermediate values for most taxa.

Table 9.5. Blue Lake: Two-way table of coincidence giving the mean relative abundances (%) of the fossil chironomid taxa in each sample cluster (Groups I, II, III), N = number of samples per group.

TAXON/GROUP	I	II	III
Chironomus	37.0	23.1	10.8
Chironomini A	9.9	4.0	5.6
Polypedilum	8.3	2.1	2.4
Riethia	1.7	2.5	1.3
Tanytarsus	0.0	0.9	2.7
Tanytarsini 2	0.0	0.8	1.9
Podonomus	7.1	6.2	3.4
Parochlus	2.9	5.2	4.7
nr. *Eukiefferiella*	11.6	17.7	30.3
Orthocl. sp. I	0.3	1.5	6.3
E. claripennis	1.0	5.1	5.0
Cricotopus sp. 4	0.3	0.8	0.8
Cricotopus sp. 12	2.7	3.4	7.8
Corynoneura	1.6	2.9	2.0
nr. *Paralimnophyes*	2.2	3.0	0.6
Orthocl. sp. III	0.5	0.7	3.4
N	6	14	9

Samples 1 to 8 which were derived from the oldest sediments of the core (Late Pleistocene samples: 407-360 cm) did not fall into any of the three groups (with the exception of 5). Samples 1 (407 cm) and 4 (402 cm) differed from all other samples (Fig. 9.6.). In sample 1 this was due to the domination of the fossil fauna by Cricotopus sp. 12 (38.5% of the total fossils in the sample) and to the sub-dominance of Podonomus (25.0% relative abundance, Fig. 9.5). Sample 4 showed the maximum abundance of Chironomus (50.0%) in the core and relatively high abundances (16.6%) of Podonomus, nr. Paralimnophyes, and Orthocladiinae sp. I.

In sample 2 (406 cm) Chironomus was dominant (25.0%), Podonomus was sub-dominant, and Orthocladiinae sp. III had 16.6% relative abundance, which was the greatest occurrence of this taxon in the core. Sample 3 (404 cm) had Podonomus (28.8%) as the dominant chironomid and Cricotopus sp. 4 (17.9%) as the sub-dominant. Podonomus (25.5%) was

also dominant in sample 6 (382 cm), whereas Chironomus was the sub-dominant taxon (17.5%). This pattern changed in sample 7 (372 cm), in which both Chironomus and nr. Eukiefferiella were dominant (19.1%) and Podonomus (17.0%) was sub-dominant. In sample 8 (362 cm) Chironomus (21.5%) remained dominant, but now Cricotopus sp. 12 (17.7%) was the sub-dominant fossil chironomid.

In the ordination analysis (reciprocal averaging) the samples are represented by points in the two-dimensional ordination diagram (Fig. 9.7.). The ordination diagram is based on the sample scores for the first two axes. The canonical correlation R (Orloci, 1978) was R(X/Y)=0.4032 for Set 1 and R(X/Y)=0.3641 for Set 2.

The ordination produced three groupings of sediment samples, which could be related to those derived from the Cluster analysis: Group I (the youngest sediments) have the highest scores on axis 2 and low scores on axis 1. These samples were dominated by Chironomus. Samples of Group II have low scores on axis 1 and lower scores on axis 2 than the samples from Group I. These samples had high abundances of Chironomus and nr. Eukiefferiella. Samples of Group III have low scores on axis 1 and the lowest scores of all three sample groups on axis 2. The dominant chironomid taxon in these samples was nr. Eukiefferiella. These results of the ordination analysis show that all Holocene samples were ordered into the two left quadrats with increasing scores on axis 2 with decreasing age of the sediments, whereas nearly all Late-Pleistocene samples were scattered in the two quadrats on the right without forming a homogenous group. The exception was sample 8 (362 cm) whose sediments were derived from close to the transition between Pleistocene and Holocene at 360 cm in the core under study (dating inferred from Raine, 1974).

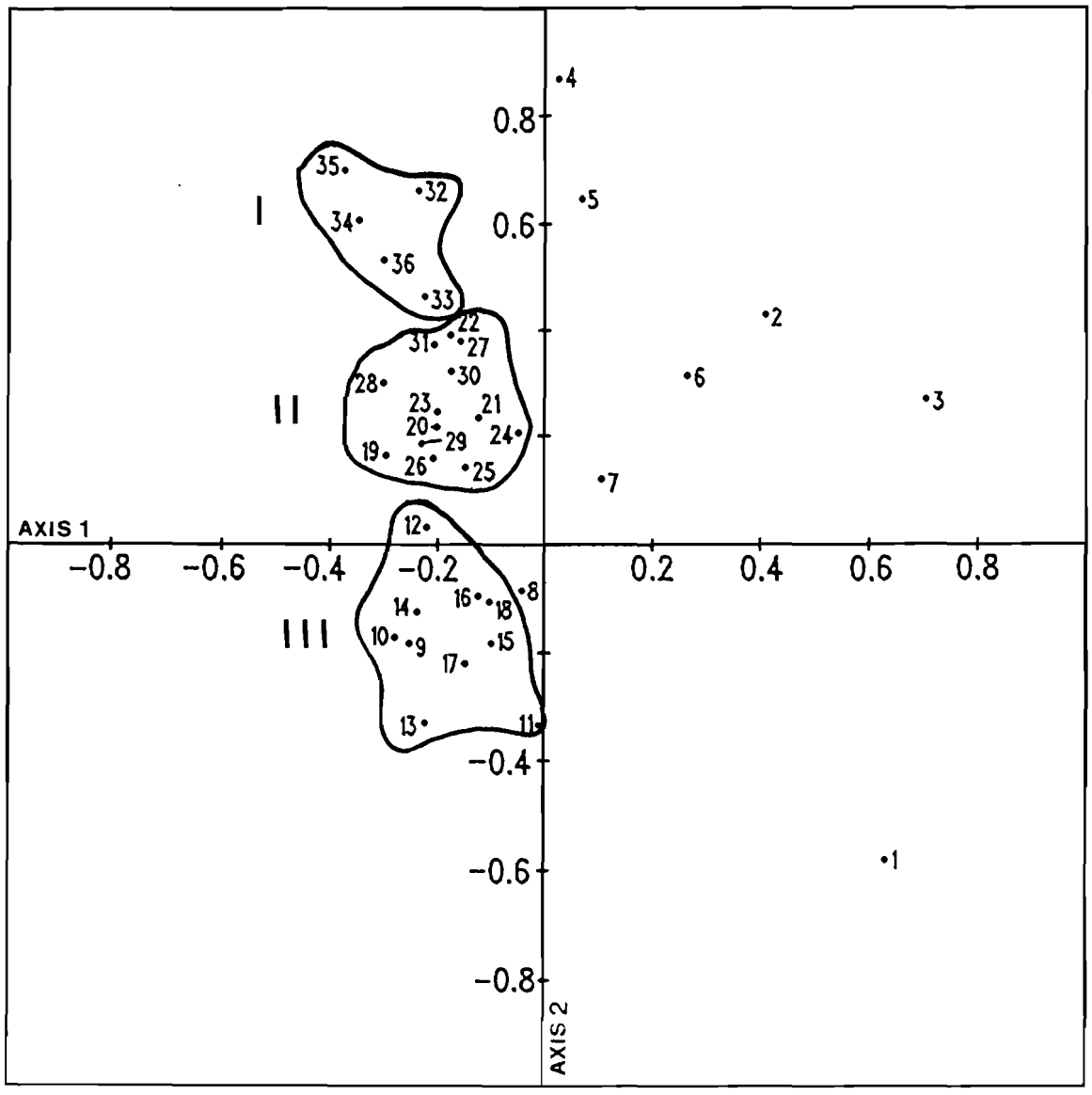


Fig. 9.7. Reciprocal averaging ordination of samples 1-36 from the Blue Lake core. The analysis is based on the relative abundance of fossil chironomid taxa in the samples. Lines on the overlay encircle groupings determined from the cluster analysis.

9.4. Discussion

The sediment core from Blue Lake covers approximately the last 13,000 years. The period constitutes the entire history of this alpine lake (with the exception of the most recent sediments covering approximately the last 1000-500 years, see section 9.2.7.) and encompasses the last centuries of the Pleistocene and most of the Holocene. In the Australian context, this lake is relatively young. Australia forms part of the earth's crust that has been relatively stable for a long period, approximately the last 60 million years. During that time, Australia did not experience major rift-type tectonism, extensive mountain range building, or as much modification of the landscape by glacial activity as occurred in the northern hemisphere or in the South Island of New Zealand (DeDeckker, 1982). Therefore, some areas in Australia have been sites of lacustrine sedimentation for long periods of time, e.g. a 20.6 m long core from a volcanic crater lake, Lake Wangoom on the edge of the Western Plains, covered the last 51,000 years (Edney et al., 1990), and lake sediments found near and south of Lake Eyre in central Australia date back to the end of the Cretaceous (Johns and Ludbrook, 1963).

Studying the relatively young sediment sequence from Blue Lake should give not only information about the developmental history of a glacial lake but also valuable zoological information. The biological aspects of interest include the biogeography of the Australian high altitude chironomids, and indicating how this fauna was able to adapt to the disturbances of glaciation and subsequent changes in macroclimate, and survive in a lake experiencing distinct seasonality. Blue Lake is more comparable to Tasmanian lakes than to most other aquatic habitats on mainland Australia, where factors such as increasing aridity or non-seasonality might be more important for the development of the fauna.

9.4.1. Zoogeographical Comparison of the Faunas of Alpine and High Latitude Freshwater Systems

To evaluate the zoogeographic position of the chironomid fauna from Blue Lake two aspects need to be discussed: firstly, the composition of the fossil fauna as represented by the fossil head capsules in the

sediment core, and secondly, the composition of the present-day fauna on the basis of the living larvae collected by Timms (1980c) and by the author (see section 9.2.6.4.).

The composition of the fossil chironomid fauna from Blue Lake shows a pronounced dominance of Orthocladiinae, a relatively high abundance of Chironomini and an unusually high percentage of Podonominae, whereas Tanytarsini and Tanypodinae are rare (Table 9.4.). High latitude and alpine aquatic environments are often dominated by Orthocladiinae, because many species of this subfamily are either cold-stenotherm or cold-tolerant (Thienemann, 1941; Oliver, 1971; Danks, 1981; Ashe et al., 1987; Roback and Coffman, 1983, 1987). The dominance of the Orthocladiinae is often not only expressed in relatively high numbers in these habitats but also in a high species diversity. In the Blue Lake fauna, Orthocladiinae had the highest number of taxa, but 50% of those taxa were so rare that their head capsules accounted for less than 1% of the total fossils found in the core.

Examples of the dominance of Orthocladiinae in high altitude and latitude environments with a similar faunal composition (on the generic or subgroup level) to that in Blue Lake can be found in lakes in the northern and southern hemispheres. Two small high altitude glacier lakes in the Low Tatras, West Carpathia, have a chironomid fauna which is mostly composed of Orthocladiinae taxa (Bitušík, 1989). Of the 28 chironomid species found in the two lakes, 18 species belong to the Orthocladiinae, one species to the Tanypodinae, three species to the Diamesinae, one species to the Prodiamesinae and four species to the Chironominae (Polypedilum and Micropsectra spp.). Lake I, which is situated in the alpine region (and therefore has a lower temperature regime), has a lower species diversity than Lake II, situated in the upper subalpine region, and also lacks the Tanypodinae and Chironomini species and 12 of the Orthocladiinae taxa.

The chironomid fauna of Thingvallavatn in Iceland is clearly dominated by Orthocladiinae in species number and abundance of larvae (Lindegaard, 1992). Most Orthocladiinae taxa have their maximum of abundance in the shallower waters except for the dominant chironomid, Heterotrissocladius, which is a profundal form and occurred down to 110 m in Thingvallavatn.

The arctic-alpine fauna of lakes in Canada includes a distinctive element formed of orthoclad species, e.g. Parakiefferiella sp. A, Paracladius, and Heterotrissocladius (Walker, 1991), besides Diamesinae and one Chironomini genus (Stictochironomus). Tanytarsus s. lat. appears to be relatively abundant in the alpine and arctic lakes studied by Walker (1991). Some genera, e.g. Chironomus and Procladius, occur in shallow, relatively warm arctic ponds, but are excluded from the colder and deeper habitats (Walker, 1991). Char Lake, a cold monomictic lake in the Canadian high arctic, with a water temperature never exceeding 4°C (Schindler et al., 1974), was inhabited by four species of Orthocladiinae, one Diamesinae and one Tanytarsini species (Welch, 1975).

In the southern hemisphere, a high proportion of Orthocladiinae was also found by Sublette and Wirth (1980) on New Zealand's subantarctic islands, where 50% of all Chironomidae species found belonged to the Orthocladiinae.

Roback and Coffman (1983) collected Chironomidae from aquatic alpine environments of the Bolivian-Peruvian altiplano. They found that Orthocladiinae were the predominant element of the fauna accounting for 60% of all species found. Most locations sampled were streams but three lakes (Titicaca, Umayo, and Chacan) were included in the collection. In Lake Titicaca, 15 chironomid taxa were recorded belonging to 10 genera. Orthocladiinae occurred with the highest diversity (nine species in five genera which amounts to 60% of the total species number), whereas Chironomini occurred with only three species in two genera (Chironomus and Polypedilum), and Tanytarsini with three species in three genera. In Lake Titicaca, Orthocladiinae and Tanytarsini were only found in the littoral zone.

The composition of the chironomid fauna of Lake Titicaca with regard to the abundance of the subgroups is similar to that of Blue Lake. In Blue Lake 61% of all chironomid taxa found belong to the Orthocladiinae, 18% to the Chironomini, but only 7% to the Tanytarsini. The difference between the two faunas is due to the presence of two taxa of Podonominae and three taxa of Tanypodinae in the fossil fauna from Blue Lake (Table 9.4.). But although these three fossil taxa of Tanypodinae were recorded, Tanypodinae appear to have

been rare throughout the history of Blue Lake as the number of their fossils accounted for less than 1% of the total.

Tanypodinae species were rare and their numerical abundance as larvae was low in Roback and Coffman's (1983) collections on the altiplano, and Tanypodinae were not recorded in studies of other high altitude lakes in the tropical Andes by Brundin (1956a). Instead the fauna in these lakes was composed of profundal Chironomus and Polypedilum species, and littoral Orthocladiinae species (e.g. Laguna Rinconada, the two Lake Lagunillas).

Further south, Tanypodinae occurred as an important element in the chironomid fauna of lowland lakes in the lake district of Chile, as well as in Patagonian lakes (Brundin, 1956a). The genus Macropelopia was most diverse and abundant in these lakes. Brundin (1956a) noted that the genus Procladius, which is widely distributed in the Holarctic, was absent from the chironomid fauna in Chile and Patagonia.

In the Blue Lake fossil fauna, Procladius, albeit rare, was the most abundant Tanypodinae taxon. In the present-day fauna, Procladius sp. was the sub-dominant chironomid found in the benthic fauna, although occurring in much lower numbers than the dominant chironomid, Chironomus oppositus. In Australia Procladius is widely distributed, together with another tanypod taxon, Paramerina levidensis. The latter taxon is also common in Australia, but it is mainly recorded from stream habitats (Pettigrove, pers. comm.). Its larvae were found only in the littoral zone of Blue Lake.

In the South Island of New Zealand, Macropelopiini are wide-spread and abundant in terms of numbers of individual larvae in standing water environments, whereas Procladius is absent. This distribution is an indication that, as was shown for the Podonominae (Brundin, 1966), some elements in New Zealand's chironomid fauna have closer relationships with the fauna in South Chile - Patagonia than with that in Australia.

It is interesting to note that two of the Chironomini taxa occurring in Blue Lake, Chironomus and, to a lesser extent, Polypedilum, appear

to be important faunal components in the profundal of some of the standing water environments in alpine regions in the southern hemisphere according to the scarce information available on these environments. The profundal of several lakes on the Bolivian-Peruvian altiplano was inhabited by species of the two genera, e.g. Laguna Rinconada (4680 m a.s.l.) and the two Lake Lagunillas (4100 m a.s.l.) (Brundin, 1956a) and Lakes Titicaca and Umayo (3815 m a.s.l.) (Roback & Coffmann, 1983). Two lakes in the Canta Valley were inhabited by three species belonging to Polypedilum, Tanytarsus, and Synorthocladius (Brundin, 1956a).

Roback and Coffman's (1987) collections of Chironomidae from freshwater environments in Nepal at altitudes between 2000 and 4000 m a.s.l. also indicated a dominance of Orthocladiinae species, which amounted to 52% of all species found. Chironomini taxa found belonged to only three genera (Chironomus, Polypedilum, and Microtendipes). Larvae of these genera were found more frequently in lentic waters (although only a very limited number of locations sampled belonged to that category), e.g. in a small pool of Kali Gandaki at an altitude of 2600 m a.s.l. (NP54 in Roback & Coffman, 1987) Chironomus sp. and Polypedilum sp. were found besides one orthoclad, Pseudosmittia sp.; and in a reservoir near Langpoghyun Khola (2830 m a.s.l.) Chironomus was found besides the Tanytarsini Micropsectra and the orthoclad Psectrocladius sordidellus.

Two species of Chironomus (C. subantarcticus and C. antipodensis) occurred in pools on the subantarctic Auckland and Campbell Islands (Sublette and Wirth, 1980), but no other Chironomini taxa were recorded.

Chironomus and Polypedilum are excluded from very cold arctic waters, e.g. Char Lake (Welsch, 1975) or other high arctic lakes in Canada (see Walker, 1991; and Walker & Mathewes, 1989), and lakes or tarns at very high altitudes, e.g. Laguna Sillacunca at an altitude of 4680 m a.s.l. in the Peruvian Andes was inhabited by only one species of Syncricotopus (Brundin, 1956a). However, Walker (1991) recorded Chironomus and Procladius as common forms in shallow arctic ponds, in which temperatures are higher than in the deeper habitats. Procladius is the sub-dominant profundal chironomid in the present-day fauna of

Blue Lake, besides Polypedilum. Thus, certain species of the three genera are adapted to cold temperatures and high altitudes, but the lower temperature limit appears to be higher than that of certain cold-adapted Orthocladiinae species.

Some Tanytarsini species in the Holarctic fauna are cold-adapted, and occur mainly in arctic waters and in alpine environments (e.g. in the European Alps). These include Lauterbornia coracina and certain species of Micropsectra (Breschtko, 1975; Welsch, 1975; Reiss, 1968). These species can also occur in the profundal of deep, oligotrophic lakes in the temperate zone. The species diversity of Tanytarsini can be relatively high, e.g. in northern Fennoscandia 40 species of Tanytarsini were recorded (Lindeberg, 1970). In southern hemisphere high altitude lakes, and in the other colder aquatic habitats, Tanytarsini appear to be generally not very common, and occur with low species diversities.

In the Andes, Brundin (1956a) recorded only three Tanytarsini species in two genera from the tropical alpine lakes he studied. A shallow lake near Huarocondo at 3800 m a.s.l., contained two species (Paratanytarsus sp. and Tanytarsus virens gr.) amongst a total of six chironomid species. Roback and Coffmann (1983) recorded four species in four Tanytarsini genera from the Bolivian-Peruvian altiplano, accounting for 7% of all chironomid species found. The Tanytarsini (three species in three genera including Tanytarsus, Rheotanytarus, and Paratanytarsus) recorded from Lakes Titicaca and Umayo occurred exclusively in the littoral. In the subantarctic islands of New Zealand, only one Tanytarsini species (Calopsectra funebris) was recorded occurring in pools on Auckland Island (Sublette & Wirth, 1980). In the fossil fauna of Blue Lake, Tanytarsini occurred with only a low relative abundance of 3.2% and were present with two taxa. In the present-day fauna of Blue Lake only Tanytarsus sp. was found in samples derived from the littoral area with a hand-net. In two of the other glacial lakes near Mt. Kosciusko, Tanytarsus sp. was present in Albina Lake and T. paskervillensis in Lake Cootapatamba (Timms, 1980c). Tanytarsus sp. also occurred in low numbers down to a water depth of 20 m in Lake Tali Karng, the only permanent natural lake in the Victorian highlands (Timms, 1974b). The benthic chironomid fauna of seven of the highland lakes in Tasmania was studied by Timms

(1978). Only one species, Tanytarsus nr. inextentus, was common and occurred in only one of the lakes studied, shallow Lake Dobson (4 m). Tanytarsus (?) sp. was common in three Tasmanian lakes studied by Fulton (1983a, b).

Podonominae occurred in the fossil chironomid fauna of Blue Lake in a relatively high relative abundance. Their head capsules accounted for 11.4% of the total fossils. Podonominae remains are usually not found in the fossil chironomid fauna from lakes in the northern hemisphere (see Hofmann, 1971a, 1978, 1991; Kansanen, 1985; Walker & Mathewes, 1987a, 1989a,b; Warwick, 1980), nor were living Podonominae larvae found in the Nepal Alpine zone by Roback and Coffman (1987). The occurrence of Podonominae remains in Blue Lake is indicative of the more southern distribution of this subfamily (with the highest species number being found in South-America; Brundin, 1966), and also of the cold-tolerance, which larvae of many species of this subfamily exhibit. The two Podonominae taxa occurring in the fossil fauna of Blue Lake were Parochlus and Podonomus. Parochlus is the most widely distributed genus and occurs in all regions of the world with the exception of Southern Africa. All four Podonominae species found on the subantarctic islands (Sublette & Wirth, 1980) belonged to Parochlus. Podonomus occurs only in South-America, Australasia, and the Neotropical region. Generally, Podonominae are cold-tolerant and polyoxybiontic. Larvae may be found in waters with a temperature range of 0-24°C (Brundin, 1966, p. 96), but many species are adapted to the lower part of the temperature range. Larvae occur predominantly in cool rivers and streams and were found in glacier torrents of different size, in the upper reaches close to the glaciers (Brundin, 1966). Larvae of some species have been found in standing water environments, e.g. Parochlus steinenii (Gercke) in meltwater tarns at high latitudes (Ashe & al., 1987), and at high altitudes, e.g. in the tropical Andes where some Podonominae species live facultatively in shallow tarns (Brundin, 1966).

The above largely descriptive account was concerned with the qualitative composition of the Chironomidae fauna of alpine and high latitude lacustrine environments worldwide, on the subgroup and partly the generic level, to investigate the biogeographical position of the chironomid fauna in Blue Lake. Factors other than biogeographical

distribution which influence species composition and quantitative abundance of the Chironomidae in standing waters, have not been considered, e.g. size and morphology of lakes or the trophic conditions in the aquatic systems in question. It can be shown that the composition of the fossil fauna of Blue Lake at least is comparable to that of similar environments: Orthocladiinae are the dominant subgroup with the highest number of species, Chironomini and Tanytarsini occur with a low species diversity, and Chironomini are often the subdominant form (especially in the profundal of lakes if very low temperatures do not limit their occurrence), whereas Tanypodinae are rare. Diamesinae, which are an important component of arctic faunas in the Holarctic, are not as common in the southern hemisphere (and are absent from the fossil and recent Blue Lake fauna).

9.4.2. The Composition of the Fossil and Recent Chironomid Fauna from Blue Lake

Although the fossil fauna from Blue Lake conforms with the composition of the chironomid fauna of similar environments at a higher taxonomic level, it also can be shown that the chironomid fauna from Blue Lake exhibits a marked degree of endemism or regionalism at the generic level in the case of the Orthocladiinae, or at the species level in some taxa of other subfamilies.

Several genera with world-wide distributions occur: Tanytarsus, Parochlus, Polypedilum, Chironomus, Cricotopus, Eukiefferiella and Corynoneura. These genera are amongst the largest chironomid genera in the world (in terms of species numbers) but are represented by very different numbers of species in Australia. The genus Tanytarsus has 26 species described in Australia but none are held in common with New Zealand (Cranston & Martin, 1989). It is not known whether the Tanytarsus taxon found in the recent and fossil fauna from Blue Lake belongs to any of the already described species, or represents a new species. The same is true for the Parochlus taxon found in the fossil fauna, even though there is only one described species of Parochlus in Australia.

In Australia the genus Polypedilum is represented by one species in the subgenus Pentapedilum, and nine species in the subgenus Polypedilum. It is possible that there are two species of Polypedilum in Blue Lake. Timms (1980c) recorded Polypedilum nr. tonnoiri from Blue Lake, but not from the other Kosciusko lakes, nor from Lake Tali Karng. This taxon was also recorded from Great Lake and Arthurs Lake in Tasmania (Fulton, 1983a) and Timms (1978) recorded two Polypedilum species from Lake St. Clair in Tasmania. The author placed the Polypedilum larvae found by her in Blue Lake nr. P. oresitrophum. This species has been recorded by Fulton (1983a) from Lake Sorell in Tasmania. Generally, Polypedilum larvae do not appear to be a common element in Australian lakes (see section 9.1.2.) and larvae of this genus have been found in only three lowland lakes, but not the above mentioned species. P. nubifer was common in Lakes Monger (Edwards, 1964) and Merrimajeel (Maher & Carpenter, 1984), and Polypedilum sp. was recorded from Lake Bullenmeri (Timms, 1981), but larvae of Polypedilum were not found in nearby Lake Purrumbete (pers. obs.). Polypedilum tonnoiri was found in all pool sites from the Yarra River studied by Pettigrove (1990).

Chironomus is represented in Australia by 11 described species (Cranston & Martin, 1989), and larvae of this genus occur in nearly all lacustrine systems studied in Australia. But the species which inhabits Blue Lake, and is the dominant chironomid of the present-day fauna, has a very restricted regional distribution in Australia. C. oppositus has been recorded only from the Kosciusko glacial lakes (Timms, 1980c), Lake Tali Karng (Timms, 1974b), and the Tasmanian highland lakes (Timms, 1978, Fulton, 1983a, b).

Of the remaining Chironomini taxa, Riethia, which accounted for only 1.8% of the total fossils in the Blue Lake fauna, was abundant or dominant in the benthic fauna of many of the Tasmanian lakes studied by Timms (1980c) and Fulton (1983a, b). Riethia stictoptera was also common in the benthos of Lake Tali Karng (Timms, 1974b) but was not recorded by Timms in his study of the benthos of the four glacial Kosciusko lakes (1980c). Fossils of this genus have been found in very low numbers in the cores from Lakes Monowai and Grasmere in the South Island of New Zealand (see Chapter IV).

In Cricotopus, three Australian species (as yet undescribed) occurred in the fossil chironomid fauna from Blue Lake. In Lake Titicaca, the Cricotopus larvae found were separated into five possible species (Roback & Coffman, 1983). Furthermore, the Cricotopus species found in New Zealand appear to be different from those found in Australia. The sole taxon of Eukiefferiella found in the Blue Lake fauna could only be identified to E. claripennis group. The same or a very close species was also recorded from the South Island of New Zealand (see Chapter IV).

There are two described species of Corynoneura in Australia, one of which is widespread also in the Holarctic and Neotropical region (C. scutellata), and the other species is endemic (C. australensis) (Cranston & Martin, 1989). Larvae of Corynoneura in Australia have been found in a variety of habitats from standing waters to fast flowing streams (Pettigrove, pers. com.). The fossils found in the fossil fauna from Blue Lake may belong to one of the described species or to a new species. In the Bolivian-Peruvian altiplano fauna, this genus was particularly numerous (represented by nine species). Roback and Coffman (1983) suggested that Corynoneurini species might fill niches in aquatic habitats on the altiplano which are occupied in similar environments in the northern hemisphere (or other parts of the world) by holarctic or near cosmopolitan orthoclad and diamesian genera that are absent from the fauna of the altiplano.

Several undescribed Orthocladiinae taxa in the fossil fauna from Blue Lake, including sp. I, sp. V and sp. XIV (see Chapter IV), possessed menti similar to some taxa found in the South Island of New Zealand. This indicates a possible close association between parts of the orthoclad fauna in the two areas. But the dominant Orthocladiinae taxon of the fossil fauna in Blue Lake appears to belong to an endemic genus with a restricted regional distribution in Australia. Pettigrove (pers. com.) collected this species from a variety of habitats exclusively in south-eastern Australia, e.g. in the upper, unpolluted, reaches of the Yarra River (Pettigrove, 1990), and in Tasmania. The habitats in Tasmania included several lakes and their tributaries in the Western Arthur Ranges and Cradle Mountains Pettigrove, pers. com.). The remaining orthoclad genera found in the Blue Lake fauna could not be associated with any of the genera described in the

literature, e.g. Orthocladiinae sp. III, sp. IV, sp. X, sp. XII, sp. XIII, Orthocladiinae/Prodiamesinae sp. and one taxon, which is similar to Paralimnophyes (Table 9.4.).

In summary, it has been shown that the chironomid fauna from Blue Lake, although possessing some world-wide and Australian-wide (Procladius, Paramerina) elements, is closely associated with the chironomid fauna in highland lakes in Tasmania.

9.4.3. Original Habitats of the Fossil Chironomid Taxa

The community structure of the present-day fauna of Blue Lake differed somewhat from the composition of the fossil fauna in the species present, and partly in quantitative aspects of the faunal composition. Timms (1980c) found only three taxa in his Ekman grab samples, with larvae of Chironomus being mostly responsible for the chironomid biomass in the lake. In the samples collected by the author (see Table 9.2.) Chironomus larvae were also the most numerous but larval densities were lower than those recorded by Timms (1980c). Both measurements of the abundance of Chironomus were derived from single visits and at slightly different times of the year. Therefore, it is not possible to determine whether the difference in densities is due to normal year-to-year variations in the lake or to recent changes in limnological conditions.

Besides Polypedilum and Procladius (also recorded by Timms, 1980c), the author recorded three additional taxa (Paramerina, Tanytarsus, and nr. Eukiefferiella) in one sample taken at a water depth of 6 m in the vicinity of the major inlet. The latter taxa were also present in the hand-net collection taken near the shore together with the four other orthoclad taxa (Table 9.2.). It therefore appears that many of the taxa which were found as fossils originated from the littoral zone of Blue Lake. The species diversity of chironomids was higher also in the littoral than in the profundal zone of Lake Grasmere (Stark, 1981) in association with the macrophyte beds. In Blue Lake, macrophytes are not present and the lake bed is mostly rocky down to at least 7 m water depth. The exceptions are deltaic sediments (mostly sands) deposited by the three influent streams. The largest of the deltaic

areas is formed by the main inflow in the north-west corner of the lake, Blue Lake Creek.

The fauna of the rocky lake bed in Blue Lake has not been studied in detail. The abundance of macrofauna on stony substrata in littoral areas of lakes can vary greatly (see Lindegaard, 1992, and references therein). Särkkä (1983) recorded abundances of macroinvertebrates on stones in 0-3 m water depth of 300 to 800 ind/m^2 in oligotrophic Lake Konnevesi, Finland. Chironomidae were the dominant macroinvertebrates and accounted for 45% of the total number of macroinvertebrates found. Epilithic algae, e.g. diatoms, on stony substrates provide the food for the zoobenthos living in the stony littoral. The diatom fauna of Blue Lake is not known, but Powling (1970) recorded Ulothrix in phytoplankton samples from Blue Lake. Ulothrix is a filamentous epilithic alga which grows attached to stones (Round, 1981) and this algae could be a possible food source for chironomids (especially Orthocladiinae) in Blue Lake's stony littoral.

The stony littoral or the littoral deltaic areas are possible habitats for some of the chironomid taxa of Blue Lake, especially the Orthocladiinae and Tanytarsini. But there is also the possibility that the fossil remains of some taxa deposited in the lake did not originate in the lake, but were transported into the lake by the inflowing streams. Such an origin is probable for the remains of Podonominae, E. claripennis, and nr. Paralimnophyes, as larvae of these two taxa were collected by hand-net from the delta of the largest inflowing stream. As can be seen in the bathymetric map of Blue Lake (Fig. 9.1.), Blue Lake Creek widens before entering the lake. This area of the creek provides at its shoreline shallow sandy habitats for chironomids (and also for taxa which prefer the littoral area if living in a lake) with a low water velocity during summer months (pers. obs.). The highest stream flows were measured in spring, due to spring thaw of snow and ice which is often accompanied by rain (Balmaks, 1984). The increased water velocity during spring could not only bring in particles (including remains of animals and live animals) from the upper reaches of the creek, but could also resuspend material deposited during the summer in the region of the delta and in the littoral of the lake, and with the stronger water velocity carry these particles far enough into the lake so that they would settle in

the deeper areas. Thus, the composition of the fossil Blue Lake fauna might be partly a reflection of the running water fauna of the inflows as well as of the fauna of the lake itself.

When considering a possible stream origin for some of the fossil taxa in the core, it appears that the average fossil density of 66.6 head capsules/ml of sediment in the Blue Lake core is quite high for an unproductive, alpine lake. The relatively high density could have been the result of a low sedimentation rate (ca. 0.02-0.08 cm/year in Raine's core, 1974, p.39). But a low sedimentation rate might suggest also that fewer particles are actually swept in from the outer regions of the lake including the stream fauna remains. Alternatively, sedimentation rates are determined by the amounts of mineral particles entering the lake and allochthonous and autochthonous organic matter. The proportion of these constituents might change during the course of the lake's development possibly influencing the concentration and composition of fossil remains. In Raine's composite core the highest sedimentation rate (ca. 0.08 cm/year) was measured between 8000 and 7000 yr B.P., whereas for most of the remainder of the Holocene the sedimentation rate was circa 0.06 cm/year. The stratigraphies of organic matter content in both cores studied were very similar (see Raine, 1974, reproduced in Appendix IV; Fig. 9.3. and Appendix, Table IV.1.). Organic matter increased considerably after 10,000 yr B.P., remained stable in the early Holocene and then increased slightly to the maximum values during the intermediate Holocene before decreasing slightly in the younger sediments with two minima occurring at ca. 3000 yr B.P. and 1700 yr B.P. in Raine's core. These two minima may have corresponded to the two low percentages of organic matter at the 100 cm and 40 cm horizon in core NA. Therefore, it appears that mineral deposition in Blue Lake decreased throughout the early Holocene (and especially that of sand; Raine, 1974, appendix IV), whereas the organic matter content increased slightly with the fraction of coarse organic matter increasing towards 7000 yr B.P. These trends were reversed in the younger sediments (see Appendix IV, Fig. 3.5). A decrease in the amount of mineral matter would mean less dilution of deposited organic matter and possibly of fossil densities in the lake. But if the organic matter, which is eventually sedimented in the deeper parts of the lake, was derived from allochthonous sources that could not only cause a dilution of the autochthonously

produced organic matter and fossil animal remains but might also suggest that fossils from the littoral or the inflow area of the lake could be transported and deposited by the same mechanism which caused the deposition of the allochthonous organic material. With the limited amount of data available for core NA, it is not possible to determine which of the above mentioned factors influenced the final composition of the fossil chironomid fauna of Blue Lake. Influx rates for chironomid remains cannot be calculated because of the lack of adequate dating of core NA and would be difficult to interpret because of possible sediment focusing (Davis et al., 1985) and differential deposition as described above.

Some examples of chironomid head capsule densities in lake cores are: Hofmann (1971a) recorded 30 head capsules/ml in core I from Schöhsee (Germany), and 5.8 head capsules/g sediment in Holocene sediments from Lac du Bouchet (France) (Hofmann, 1991). Warwick (1981) found 4.6 to 123.8 specimens per cm^3 (ml) of sediment for the Glenora B core he studied. Walker and Mathewes (1989a) needed to analyse sediment amounts up to 93 ml to obtain 50 head capsules for an analysis of the chironomid remains in surficial sediments of glacial, unproductive lakes in Canada. The author had to use ca. 50 ml or more of wet sediment from large unproductive lakes in the South Island of New Zealand to obtain at least 50 head capsules for the lake survey described in Chapter VIII. Therefore, this suggests that in comparison with other lakes, Blue Lake has a relatively high density of fossil chironomid remains, possibly originating from the littoral area of the lake. But if many of the Orthocladiinae and Podonominae remains found in the core were indeed stream-derived that would mean that the populations from which the fossils originated would have been either small in-lake populations or comparatively large upstream populations in order to achieve some of the faunal compositions in the samples from the Blue Lake core, e.g. higher numbers and relative abundances of Orthocladiinae and Podonominae especially in some samples from the Pleistocene and older Holocene (Fig. 9.4. and Appendix, Tables IV.2., IV.3.). The possibility of a stream-derived chironomid fauna has to be taken into account when interpreting the fossil chironomid data.

I believe that in some taxa there may not be an exclusive preference for either habitat, running waters or the littoral zone. Examples of

taxa occurring in both habitats are nr. Eukiefferiella SRV sp. 38, Polypedilum tonnoiri, and Riethia stictoptera, which have been recorded from Lake Tali Karng (Timms, 1974) and from the Upper Yarra (Pettigrove, 1990). Some chironomid taxa in the South Island of New Zealand have also have been collected from both habitats, e.g. Paucispinigera approximata (see Chapter V) and Paucispinigera sp. a, which was found in Lakes Monowai, Matheson, and Tekapo, and in streams on the Banks Peninsula (Coll. R.L.C. Pilgrim, unpubl. data), as well as Tanytarsus vespertinus and Paratanytarsus, which occurred in Lake Grasmere and in streams in the Cass region (Coll. R. Death, unpubl. data). Similar results have also been recorded from other regions of the world. Bitušík (1989) found several Orthocladiinae and Diamesinae species in stagnant waters in the Low Tatra, which were considered originally to be exclusively rheophil species. He suggested that many of the rheophil species can live and develop in stagnant waters with high concentrations of dissolved oxygen. This has been confirmed by other authors studying high altitude lacustrine systems in the High Tatras (Ertlová, 1987) and in the Sierra Nevada (Laville & Vilchez-Quero, 1986).

9.4.4. Climate and Sedimentation Regime in Blue Lake

The community structure of the fossil chironomid fauna from the sediment core from Blue Lake, as analysed by the classification and ordination technique (Fig.s 9.6. and 9.7.) showed several shifts in the dominance pattern during the last 13,000 years of the lakes's developmental history. The fossil fauna of the oldest sediments (407 to 362 cm) showed changes in the relative abundance of the dominant chironomid taxa from sample to sample and was therefore not classified as a sediment group. These sediments were deposited in the late-Pleistocene according to the correlation of core NA with Raine's (1974) cores from Blue Lake (see section 9.2.7.). Following the dating of the sediments in Raine's cores, the top of zone D at 360 cm in the core under study (Fig. 9.2.) would have been deposited ca. 10,000 yr B.P., and the top of zone C at 334 cm ca. 9000 yr B.P. The sediments deposited in the Holocene were divided by the numerical analyses into three sediment sequences according to the percentage composition of the fossil chironomid fauna. Group III encompasses the sediments from

352 to 242 cm, Group II the sediments from 223 to 60 cm, and Group I the sediments from 40 cm to the top of the core. The sediments of Group I were deposited after 1700 yr B.P. (Table 9.3.), but the timing of the transition between Groups III and II is uncertain because there is no date available from the intermediate part of core NA.

Sediments were not deposited evenly over the lake floor in Blue Lake, but instead sediment focussing (a pattern of differential deposition; Davies et al., 1985) occurred. Both cores from Blue Lake were derived from the basin near the centre of the lake but whereas core NA, cored at a water depth of 24.5 m, yielded a sediment length of 446 cm, Raine's composite core was obtained from the deepest part of the basin (26 m) and yielded a sediment length of 680 cm. Considering the good correlation in the stratigraphies of the older sediments of the cores, and assuming that sediment focusing was a continuous process throughout the Holocene, it is possible that the sedimentation rate at the site of core NA would be proportionally less than that of Raine's core. The date of 6000 yr B.P. is located at approximately the middle of Raine's core and with a lower proportional sedimentation rate, this would place 6000 yr B.P. approximately between 210 and 230 cm in core NA. This speculative date will be used to interpret the sediment sequences derived from the numerical analyses. The development of the fossil chironomid fauna will be described according to the sediment sequences defined above.

The available sediment record from Blue Lake covers a period of several changes in macroclimate. After the disappearance of the ice from the Blue Lake cirque at some time between 15,000 and 14,000 yr B.P. (Raine, 1974; Bowler et al., 1976), deposition of organic and lacustrine material began ca. 13,000 yr B.P. The first planktic pollen were recovered by Raine (1974) at this time. Climatic amelioration (increase in temperature and available moisture) was such that by 8700 yr B.P. herbaceous plants were replaced by wet sclerophyll forest taxa as the treeline rose to its present level (Raine, 1974). Macphail (1983) indicated that early Holocene temperatures might not have risen substantially above present-day values but that temperature variability was reduced resulting in effectively warmer conditions. The maximum expansion of woody taxa occurred in the Snowy Mountains between 8600 and 6700 yr B.P. After 6500 yr B.P. precipitation started

to decline and the climate became similar to the present conditions, with the exception of the cold phase between 3800 and 1500 yr B.P. when temperatures and precipitation declined to a minimum (Raine, 1974; Bowler et al., 1976).

The sediment sequences derived from the numerical analyses closely correlate with the major changes in climate. The sediment sequence III began with the Holocene and most samples contained in this sequence would have been deposited during the warmest phase of the Holocene. The timing of the transition between sediment sequence III and II is not certain, but it can be said (see page 13) that most samples of sequence II were deposited during the cooling and drying phase of the Holocene (after 6500 yr B.P.) which reached a maximum between 3800 and 1500 yr B.P., after which conditions developed again similar to the present climate. The last change is represented by sediment sequence I, which includes the youngest sediment samples from 40 cm to the top of the core.

9.4.5. Stratigraphies of the Most Abundant Fossil Chironomidae

Using fossil chironomids to gain information about the developmental history of Blue Lake meets the same difficulties as were described for the interpretation of the fossil fauna from Lake Grasmere in New Zealand (Chapter V) i.e., a relatively high number of undescribed taxa and sparse ecological information about chironomid taxa in Australia. However, there is some ecological information available concerning the most abundant taxa, and additionally, the shifts in the dominance patterns of the fossil chironomids occurred more or less in accordance with changes in macroclimate. Temperature was one of the main factors which changed with time and appears to have been also one of the major factors determining the community structure of the chironomids throughout the history of Blue Lake, either directly or indirectly (e.g. through changes in the available food supply). Temperature is a very important factor in alpine environments (Bitušík, 1989; Walker et al., 1991) and chironomids are known to respond to both temperature and daylength (Rossaro, 1991b). Additionally, the type of substrate available appears to have influenced the fossil chironomid fauna in Blue Lake.

It is unlikely that major changes in trophic state would have been important for the succession of the fossil chironomid fauna. As the recently measured limnological data show (see section 9.2.), the lake is still oligotrophic and unproductive with regard to nutrient loading and phytoplankton development. Only one colony of Dinobryon was found in a phytoplankton sample taken by the author. Dinobryon is cold-adapted and has been found in arctic (Round, 1981) and alpine lakes (Thomasson, 1956). Raine (1974, Fig. 3.12, p. 116) recorded as the dominant aquatic taxon 'Sphere-W' which was most abundant during the late-Pleistocene, occurred with lower abundances between ca. 8700 and 5000 yr B.P. and increased again after 5000 yr B.P. In addition, Raine (1974) recorded Botryococcus braunii, in lower numbers than 'Sphere-W', throughout the Holocene with a maximum during the early Holocene. Round (1981, p. 267) listed B. braunii as one of the dominant algae in the eutrophic Irish Lough Cullin. The maximum of B. braunii during the early phase of the Holocene, which was also the warmest phase, might point to a slight increase in lake productivity during that time. All other aquatic taxa were rare or did not occur continuously during the Holocene.

In the core from Blue Lake, the oldest deposited sediments consisted of clay and silt, containing neither chironomid remains nor aquatic pollen. Loss-on-ignition was very low (Fig. 9.3.), but increased from 2.9% of dry weight in the 441 cm sample (Appendix, Table IV.I) to 6.2% in the 408 cm sample, which marks the beginning of organic deposition in the lake. During the late-Pleistocene, the content of organic matter rose to 13.5% near the Holocene transition and to 24.0% in the 338 cm sample which was deposited approximately 9000 yr B.P. The exception was a short-termed decline of the organic matter content near zone F at 403 cm (Fig.s 9.2. and 9.3.).

The first chironomid head capsules were recovered from the 407 cm sample (13 head capsules comprising 5 taxa, Fig. 9.4. and Table IV.2. in the Appendix). Numbers of chironomid remains in the samples, as well as the numbers of taxa present, increased with increasing organic matter content of the sediments. Coinciding with the short-term decline in organic matter at the 403 cm level, both parameters declined to a minimum (six head capsules belonging to four taxa). The decline in the water content in the 403 cm sample together with the

lowered content of organic matter points to increased minerogenous input for a short time at approximately 12,000 yr B.P. This mineral input caused the lower abundance and diversity of the fossil chironomids either by the effects described for Lake Grasmere (Chapter V; e.g. interference with substrate or food matter) or by diluting the amounts of remains through the sedimentation rate which may have been high at that time.

Temperatures during the late-Pleistocene were still low (5°C below present, but increasing towards the Holocene (Kershaw et al., 1983)) and the sedimentary conditions unstable, which is shown by the colour changes in the core lithography (Fig. 9.2.; the late-Pleistocene encompasses sediment zones H, G, F, E, and D) and the input of sand particles in zone F. These conditions were not only reflected in the composition of the fossil chironomid fauna, but also by the lowest average fossil density and species number compared with those of the three periods of the Holocene and determined by the numerical analyses. The eight samples from the Pleistocene, which contained chironomid remains, had an average fossil density of 32 head capsules per ml of sediment and a mean species number of 8.3 chironomid taxa per sample (Appendix, Table IV.2).

Two taxa, Podonomus and Chironomus, were not only amongst the first taxa to colonize Blue Lake (or being deposited as fossils in the lake) but also occurred in all samples derived from the late-Pleistocene. Besides Chironomus and Podonomus, Riethia, E. claripennis, and Cricotopus sp. 12. were the first chironomid taxa to colonize Blue Lake. The latter three taxa were not found in the next sample, but occurred sporadically in later samples of the late-Pleistocene.

All taxa, which accounted for more than 1% of the total fossils, appeared at some time during the Pleistocene, e.g. nr. Eukiefferiella was first found in the 406 cm sample together with Orthocladiinae sp. I and III, and Corynoneura and nr. Paralimnophyes appeared for the first time in the fossil fauna at the 404 cm horizon. Of the rare taxa in the fossil fauna from Blue Lake, only Cricotopus annuliventris gr., Orthocladiinae IV, V, XII, XIII, Xenochironomus, and Tanypodinae sp. I were not found in the Pleistocene. Head capsules of Paramerina were found in the 392 cm sample, whereas Procladius belonged to the

late colonizers of the lake and appeared at the 362 cm horizon close to the transition to the Holocene. Polypedilum and Tanytarsus also belonged in this group and were found in the 362 cm sample and the 372 cm sample respectively (Appendix, Table IV.3.). Thus even with the low temperatures prevalent during the Pleistocene, most chironomid taxa of the fossil fauna from Blue Lake were able, if only in small numbers, to survive in the lake or in the inflows at that time.

The cold-adapted or cold-tolerant Podonomus was clearly the most abundant taxon during this period together with Chironomus. These two taxa were alternately dominant during the late-Pleistocene (Fig. 9.5.). As described earlier, Podonominae larvae can survive and develop to maturity in very cold and rather extreme freshwater environments (e.g. in glacier torrents) so that the high relative abundance of a Podonominae taxon during the coldest and most unstable period of the lake's developmental history would be expected. There are two possibilities for the origin of these fossils: they could have been carried into the lake by one of the inflows (in which case the original stream population of Podonomus would have been relatively larger than the in-lake population of chironomids) or the larvae of this taxon might have colonized the lake due to the very low temperatures prevalent during the late-Pleistocene.

The second taxon which was dominant during the Pleistocene, Chironomus oppositus, can be regarded as a cold-adapted taxon compared to other species of Chironomus, as is shown by its present distribution in highland lakes in mainland Australia and Tasmania. In Tasmania C. oppositus has only been recorded from the deep highland glacial lakes (St. Clair and Dove in Timms' study; 1978) and not from the shallow lakes or reservoirs from lower elevation areas (Timms, 1978). Fulton (1983a,b) recorded C. oppositus from three lakes in the alpine area of the Central Plateau in Tasmania: Great Lake, Arthurs Lake, and Lake Sorell.

The cold-adaptation of C. oppositus has to be seen in the context of the actual physical conditions of the alpine environments which this species is inhabiting. Since alpine environments vary in elevation and latitude, which are the macrogradients determining the physical factors prevalent in alpine systems, such as solar radiation received,

the day-length, temperature, and amounts of precipitation - these environments differ from each other depending on their geographical location and elevation (Billing, 1979). At 36° S latitude and 1890 m a.s.l. elevation, Blue Lake does not experience climatic conditions quite as severe as, for example, some arctic lakes (e.g. Char Lake; Schindler et al., 1974) in which water temperatures may not rise above 4° C. In present day Blue Lake, ice cover of the lake lasts for about five to six months, but summer temperatures can reach 13.7° C in February (average water temperature of the surface waters; Balmaks, 1984). Although the lower temperature limits for the development of C. oppositus are not known, it appears that the relatively high summer temperatures for an alpine lake shown by Blue Lake allowed the development of this taxon throughout the past (Fig. 9.5.). There is also the possibility that C. oppositus lived in the shallower area of the lake during the cold Pleistocene. Considering the present day distribution of this taxon, there may be an adaptation or a preference for lower temperature conditions than other Chironomus species. The temperate profundal larvae of Chironomus plumosus may not feed below 5° C (Hilsenhoff, 1966) and the temperate midge Chironomus salinarius does not complete emergence at temperatures below 13° C at the northern limit of its range (Koskinen, 1968). These and lower temperatures occur in the Blue Lake environment, and as C. oppositus remains the dominant profundal form in the chironomid fauna, relatively low temperatures are not restricting for this taxon.

Temperature regimes in the Tasmanian alpine lakes, in which C. oppositus occurs, are higher and exhibit a greater range than those measured for Blue Lake. On the Central Plateau the large unstratified lakes at high elevation (Great Lake at 1030 m a.s.l. and Arthurs Lake at 952 m a.s.l.) have a temperature range of the surface waters of 2° C to 19° C (whereas the lowest winter temperatures measured in Lake Sorell, at 820 m a.s.l., never fell below 3° C). These lakes occasionally freeze over during extreme winters. Lake St. Clair (737 m a.s.l.) had a temperature range of 5.6 to 19.8° C. It was suggested that the great depth of this lake (120 m) limited the range of seasonal variation (Tyler, 1974, and references therein). It is interesting to note that with the higher temperature ranges in the Tasmanian lakes, the abundance of larvae of C. oppositus appears to be lower than in Blue Lake, and the same seems to be true for most of the

other lakes in mainland Australia from which this species was recorded. Timms (1980c) listed larval densities of C. oppositus of 1132 to 3951 individuals m^{-2} in Blue Lake. Larvae of this taxon accounted for 98.8% of all chironomids found in his samples (calculated from Timms (1980c) abundance data). In Lake Tali Karng, larval densities ranged from 0 to 260 in the samples and C. oppositus accounted for only 15.4% of the total number of larvae (Timms, 1978). In the two Tasmanian lakes in which Timms (1978) found this species, C. oppositus larvae accounted for only 2.1% of the total number of chironomid larvae found in Lake St. Clair; and for 24.9% in Lake Dove (calculated from Timms (1978) abundance data). Fulton (1983b) recorded C. oppositus as common (101-1000 individuals m^{-2}) in only one sample site in Great Lake and Arthurs Lake, respectively, whereas larvae of this species were rare in Lake Sorell (Fulton, 1983a). Arthurs Lake is generally warmer than Great Lake by about 2 to 3° C, probably because it is at a slightly lower altitude and is more sheltered. The overall abundance of C. oppositus in Arthurs Lake is lower than it is in Great Lake (Fulton, 1983a,b). These data might indicate a preference for colder temperatures of this taxon.

By the time the 362 cm sample was deposited (close to the transition to the Holocene), the organic matter content of the sediments had increased to 13.5%, and the water content to 67.6% (Fig. 9.3.) indicating less compact sediments. The number of chironomid remains increased to 79 belonging to 12 taxa. The relative abundance of Chironomus was still high (21.5%), but that of Podonomus declined to 5.1%, and the relative abundance of nr. Eukiefferiella was still low (5.1%). The transition to the Holocene in the following sample was reflected by considerable changes in the community structure of the fossil chironomid fauna. The sediments of the early Holocene (352-242 cm) have been clustered into sediment group III by the classification analysis (Fig. 9.6. and Table 9.5.). The average fossil density of the samples of this period increased to 102 head capsules per ml of sediment and the mean taxa number was 17.3 chironomid taxa per sample. These values are the highest in the core and indicate that the production and diversity of chironomids in Blue Lake reached their maximum development during the warmest phase of the Holocene.

In the first sample of the Holocene (352 cm), changes in several

parameters not only marked the transition from the Pleistocene but some of these parameters also reached their maximum in the core. Loss-on-ignition increased to over 20% of dry weight and increased throughout this period to 30% in the 243 cm sample. The number of head capsules reached the maximum in the core with 188 head capsules retrieved from this sample. The species diversity of 22 taxa was also the maximum number found in the core. These pronounced peaks in fossil density and species numbers appeared to be a singular occurrence and not an indication of actual faunal development because both parameters declined in the following samples to stabilize after 9000 yr B.P. (Fig. 9.4. and Appendix, Table, IV.2.) at a lower plateau. The higher fossil density and species diversity in all of the early Holocene samples indicated climatic amelioration with the warmest period of the Holocene occurring after 8700 yr B.P., when the treeline had risen to its present levels. The increase in temperature might have increased the autochthonous production in the lake, as indicated by the increase in Botryococcus spores (Raine, 1974). But even considering the climatic amelioration and the possible increase in lake productivity, the sudden peak in numbers of remains and fossil taxa in this one sample (352 cm), deposited after 10,000 yr B.P. and possibly before 9500 yr B.P., is difficult to explain. A possible explanation might be that although the in-lake population of chironomids was growing quickly at that time, the sedimentation rate was still lower than later in the early Holocene (the highest sedimentation rate was recorded by Raine (1974) ca. 8000 yr B.P.) so that dilution of the fossil density was low compared with that in the following samples.

The dominance pattern of the fossil chironomid fauna changed in the 352 cm sample and the same community structure was essentially maintained for the remainder of the sediment sequence. This change in the fossil chironomid fauna at the beginning of the Holocene might also point to a very quick response of the aquatic fauna to an increase in temperature, as was suggested by Walker et al. (1991).

Nr. Eukiefferiella became the dominant taxon in the fossil chironomid fauna and remained dominant in every sample up to the 242 cm horizon (sediment group III, see Table 9.5. and Fig. 9.5.). The relative abundance of Chironomus declined and remained low throughout this period with two minima of occurrence in the 322 and 282 cm sample.

Also the relative abundance of Podonomus declined and was at its lowest level in this period of the Holocene (Fig. 9.5. and Table 9.5.). Both taxa of the Tanytarsini, Tanytarsus and Tanytarsini sp. 1, which had been rare in the Pleistocene samples, were found in small numbers in nearly every sample and had their highest relative abundance in this part of the core (Table 9.5. and Fig. 9.5.). Of the Tanypodinae taxa, Procladius and Tanypodinae sp. I, occurred only sporadically, but Paramerina was found in low numbers continuously through this period (Appendix, Table IV.3.). Therefore it appears that the abundances of the more cold-adapted chironomid taxa decreased considerably in the early Holocene compared with the Pleistocene, and that taxa which are generally more abundant in warmer waters, e.g. the Tanytarsini and Tanypodinae, increased slightly, or in the case of nr. Eukiefferiella, became the dominant taxon.

The geographical distribution of nr. Eukiefferiella in Australia is limited, as is that of C. oppositus, although the variety of aquatic habitats inhabited by nr. Eukiefferiella appears to be larger than that of C. oppositus. Nr. Eukiefferiella may be restricted to south-eastern Australia. It has been collected from many Victorian streams (Pettigrove, pers. com.) and was one of the dominant chironomids in the upper reaches of the Yarra River (Pettigrove, 1990). This taxon also occurs in lakes and streams in the Western Arthur Ranges and Cradle Mountains in Tasmania. A dietary analysis indicated that nr. Eukiefferiella predominantly feeds on benthic diatoms, although it is not an obligatory herbivore and can feed on detritus. It was suggested that the distribution of this taxon could be influenced by the amount of benthic diatoms present in its habitat. In more polluted areas of streams (such as site 110 Dights Falls in the Yarra River (Pettigrove, 1990)) unpalatable types of algae might be present which restrict the occurrence of nr. Eukiefferiella (Pettigrove, pers. com.).

Contrary to C. oppositus, which appears to be restricted to highland lakes, nr. Eukiefferiella occurs in a wider range of altitudes and at lower elevations than C. oppositus, which may mean that this taxon is more warm-adapted and has a higher optimal temperature than C. oppositus.

There are two possible explanations for the changes in the chironomid

fauna occurring at or near the Pleistocene/Holocene boundary, temperature changes and trophic alterations. With the climatic amelioration at the close of the Pleistocene, summer water temperatures would have increased, restricting more cold-adapted chironomids to either the deepest parts of a lake (if thermally stratified) or the vicinity of cold springs (Walker & Mathewes, 1987). The summer stratification in present-day Blue Lake may only develop for a short time or during relatively calm summers. With the less variable climatic conditions prevalent during the early Holocene summer stratification may have developed more regularly and might have been maintained for a longer period. Considering that C. oppositus is very abundant in present-day Blue Lake, it appears that even with a possible stable summer stratification the lake did not offer the right conditions (possibly not low enough temperatures) during the early Holocene to ensure high abundances of this taxon. During this period the relative abundance of Podonomus was lower than that of C. oppositus (Table 9.5., sediment group III), possibly indicating an increased distance of the habitat of this taxon upstream from the lake and/or a smaller population producing the fossil remains.

The pronounced increase of numbers of head capsules and relative abundance of nr. Eukiefferiella during the early Holocene might point to a positive response of this taxon to the increase in temperatures. The higher abundance might have been caused not only by rising temperatures but also by a change in trophic state, which might have caused a general increase in algal production, and more specifically, an increase in the growth of benthic diatoms favoured by nr. Eukiefferiella.

Temperature can influence both autochthonous and allochthonous productivity. Higher temperatures might also facilitate more rapid chemical weathering of catchment materials releasing plant nutrients such as phosphorus and increasing primary productivity in the lake (Walker & Mathewes, 1987). An indication for slightly higher productivity in Blue Lake could be seen in the maximum of Botryococcus braunii during the early Holocene (Raine, 1974). Fossil diatoms from Blue Lake have not been studied so that it has to be inferred from other algal groups that there might have been more benthic diatoms available to sustain a relatively large population of nr.

Eukiefferiella during the early Holocene.

Some of the other Orthocladiinae taxa reached their maximum abundance in the sediment sequence III, especially Orthocladiinae sp. I and III, and Cricotopus sp. 12 indicating possibly better conditions in the food supply of these taxa (e.g. benthic diatoms or other algae groups). Therefore, temperature might have been mainly responsible for the observed faunal changes from Pleistocene to Holocene through direct effects upon organisms and indirect regulation of lake productivity (Walker & Mathewes, 1987; Sweeney et al., 1992).

After 6500 yr B.P. macroclimate began to change. The trends in climate were towards greater contrast in extremes of weather and greater annual variability especially with colder winters (McGlone et al., 1992). These patterns were well established by 3000 yr B.P. In the Snowy Mountains, cold and dry conditions appear to have reached a maximum between 3800 and 1500 yr B.P. As was mentioned earlier, most samples of the sediment sequence II were possibly deposited close to or after the change in climatic conditions. The sediment group II is represented by the 223 to 60 cm samples in the core. The organic matter and the water content of the sediments above the 223 cm horizon increased slightly from the values reached during the early Holocene (Fig. 9.3., Appendix Table IV.1.). This is possibly due to an increase of coarse organic matter, which in Raine's core (1974) was generally higher during the later Holocene. The increase of coarse organic matter might point to a higher input of allochthonous organic matter during this period, caused by the greater environmental variability. The fossil densities in these sediment layers were lower than during the early Holocene with an average of 70 fossil head capsules per ml of sediment. The mean taxa number declined slightly to 15.3 taxa per sample (Appendix, Table IV.2). During this period there was, however, a single peak of abundance at the 221 cm horizon. This sample contained 148 fossil head capsules belonging to 19 taxa, which represented the second maximum in the core (Fig. 9.4.). I cannot suggest an explanation for this isolated increase of fossil chironomid remains, especially with the pattern of the relative abundances of the taxa being in accordance with those of the remaining samples of this period.

For the first part of the sediment sequence Orthocladiinae remains were slightly more numerous in the samples (Fig. 9.4.) but this changed above the 140 cm horizon, when Chironomini became the dominant group in the samples and remained dominant up to the top of the core. Despite the dominance of the Orthocladiinae in the sediments from 223 to 140 cm, the dominance pattern of the fossil chironomid taxa, which was more or less prevalent during this sediment sequence, was already established in the 223 cm sample. As Fig. 9.5. shows (see also Table 9.5.) the relative abundance of nr. Eukiefferiella declined and this taxon became the sub-dominant chironomid in sediment group II. Corresponding with that decline, there was also a slight decrease in the relative abundances of several other Orthocladiinae taxa in sediment group II, especially those of Orthocladiinae sp. I, Cricotopus sp. 12, and Orthocladiinae sp. III. Both Tanytarsini taxa were rare during this period, whereas the relative abundance of the cold-adapted Podonomus increased. Chironomus, which was sub-dominant during the early Holocene, became the dominant fossil chironomid in the fauna of this period. The exceptions were the 160 and 80 cm samples in which nr. Eukiefferiella was dominant.

The factors which were responsible for this change in the dominance pattern during the late Holocene might, ultimately, have been changes in climate. Botryococcus spores, albeit still present throughout the remainder of the Holocene, declined in abundance after 7000 yr B.P. (Raine, 1974). This decline might indicate a reduction of the in-lake productivity, possibly caused by overall cooler temperatures. With a generally lower lake productivity, nr. Eukiefferiella's preferred food supply of specific benthic diatoms might have been reduced, which in combination with lower temperatures (or especially colder and possibly longer winters), might have caused the lower numbers of this taxon in the samples of sediment group II. In this context, the relatively high abundances of nr. Eukiefferiella in the 160, 100 and 80 cm samples are somewhat unusual (Fig. 9.5.). The slightly higher numbers of nr. Eukiefferiella in these samples might be due to normal variation; but if these higher abundances represented a trend in faunal structures at these times, then factors other than temperature or food substrate (and as yet unknown) might have been responsible for the faunal composition in these samples. This might be especially true for the 100 and 80 cm samples, which were possibly deposited after 3000 yr

B.P., when this area of the Snowy Mountains was experiencing a cold phase (Costin, 1972).

Raine (1974) recorded minima in the water and organic matter content (corresponding possibly with the minima at 100 cm and 40 cm in core NA), and in the amount of coarse organic material at approximately 3000 yr B.P. and then again at 1700 yr B.P. These minima indicate more compact sediments, an increase in minerogenous allochthonous matter, and a possible decrease of allochthonous organic matter for two short periods, both of them associated with the cold phase. The appearance of a small fraction of sand particles in the younger sediments (Raine, 1974; Fig. 3.5, Appendix IV) also points to an increase of erosion in the catchment of the lake. If there was a greater amount of minerogenous allochthonous matter coming into the lake via the inflows, this might have had less influence on the littoral region of the lake (which was a possible habitat of nr. Eukiefferiella), but instead might have interfered with the substrate or food matter of the profundal chironomids, e.g. Chironomus. This might have been reflected in the changes of the relative abundances of the two taxa. In the 100 and 80 cm samples, the relative abundance of Chironomus declined (from 28.0% at 120 cm to 24.0% and 21.2% at 100 and 80 cm respectively), whereas the relative abundance of nr. Eukiefferiella increased (from 12.0% at 120 cm to 21.3% and 24.0% at 100 and 80 cm respectively). In the following sample (70 cm), the relative abundances returned to predisturbance level and that of nr. Eukiefferiella decreased even further in the following samples (Fig. 9.5.).

Whereas the cooler temperatures or colder and possibly longer winters during the later Holocene might have restricted the abundance of nr. Eukiefferiella to some degree, they might have been more favourable for the occurrence of Chironomus, partly causing the increase of its relative abundance in the sediments of group II. Additionally, the type of substrate might have influenced the growth of this taxon. In most lakes studied, which had populations of Chironomus oppositus, larvae of this taxon were most abundant in detritus-laden mud or in sediments with a relatively high percentage of organic matter. In Lake Tali Karng (Timms, 1974b) C. oppositus is the dominant profundal chironomid, but it occurred mainly in that part of the lake where sediments were highly organic (e.g. 32% organic matter at 45 m water

depth). Lake Tali Karng received a considerable amount of allochthonous organic material (in the form of woody detritus) and Timms (1974b; p. 278) states that "the benthos of Lake Tali Karng is largely supported by allochthonous matter rather than by autochthonous detritus derived from the plankton". This situation appears to be similar to that in Blue Lake, where Timms (1980c) regularly recovered partly decomposed leaves and twigs from samples, pointing to input of organic matter from terrestrial sources. As Blue Lake is still an unproductive lake by such criteria as water chemistry and the sparse phytoplankton development, but supports a relatively large population of Chironomus oppositus, the allochthonous organic material appears to provide the food matter for this chironomid. This taxon is a surface feeding detrivore and therefore favours highly organic mud or might even be capable of utilizing coarser allochthonous organic matter.

In the Tasmanian lakes, larvae of Chironomus oppositus were more numerous at sampling stations which had a relatively high percentage of organic matter. In Lake St. Clair this taxon occurred in higher numbers at the northern end of the lake in detritus-laden mud and in Lake Dove, larvae of this taxon were abundant in organically rich profundal mud (24% organic matter) and at the southern end of the lake where the sediments contained appreciable amounts of leaves and twigs (Timms, 1978). The distribution of C. oppositus in Great Lake and Arthurs Lake was clearly influenced by the amount of organic matter in the sediments. Both lakes were originally shallow and consisted of separate basins or lakes, which were united when water levels were raised. These changes produced two identifiable levels in the lakes, the original and new level. In both lakes, the substrates of the old levels were generally clays with a surface layer of brown silt. In samples of these sediments C. oppositus was rare or absent. The substrates of the new levels contained considerably greater amounts of organic matter, sometimes with recognisable terrestrial organic material. In Arthurs Lake, this taxon was only found in samples from the new level and most abundant at NA1, where a proportion of 39.1% of the sediments was organic matter. In Great Lake, C. oppositus was found at all sampling stations from the new level and was most abundant at NG3 (15.0% organic matter) (Fulton, 1983b).

In the sediments of group II, the organic matter content reached its

maximum and this was possibly due to an increase of coarse organic matter (Raine, 1974) which could have been derived from terrestrial sources. The high content of organic matter during this period would have supported the possible increase in the population size of C. oppositus as shown by its higher relative abundances. During the warmer phase of the earlier Holocene the organic matter content of the sediments was already relatively high, but the lake supported a proportionally small population of C. oppositus (in comparison with that of nr. Eukiefferiella) pointing to the possibly negative influence of the warmer temperatures on this taxon.

The most recent period in the core, as represented by the sediment sequence I (40 cm to the top of the core), encompassed the time from ca. 1700 yr B.P. (see Table 9.3.) to approximately 500 -1000 yr B.P. (due to the loss of the top sediments in the core). The average fossil density of this period was again lower (47 head capsules per ml of sediment) than that of the period before and also the mean taxa number was lowered (9.5 taxa per samples). These values approach those of the Pleistocene samples. There was a minimum in organic matter content of the sediments at 40 cm, and the overall amount of organic matter declined slightly (Fig. 9.3.). The samples of the sediment sequence I were grouped together because of a further increase in the relative abundance of Chironomus and a decrease in the relative abundance of nr. Eukiefferiella (Table 9.5.). Most Orthocladiinae taxa had their minimum occurrence during this period, whereas no Tanytarsini remains were found in the samples. The relative abundances of cold-adapted Podonomus, Polypedilum, and Chironomini A were the highest in the core (Fig. 9.5. and Table 9.5.).

The 40 cm sample was deposited ca. 1700 yr B.P., close to the end of the cold phase. Precipitation and possibly temperatures (which might have been lower than today during the cold phase, Costin, 1972) increased after 1500 yr B.P. towards present-day conditions. The coarse organic matter fraction was at a minimum ca. 1700 yr B.P. but increased in the later sediments, whereas the amount of sand slightly declined (Raine, 1974). The lower fossil densities and the lower taxa numbers of sediment sequence I give the impression of a destabilized fauna. Only numbers of Chironomus head capsules remained relatively high in the samples, whereas the number of remains of most other taxa

declined, causing the high relative abundances of Chironomus during this period. It is difficult to imagine what caused the decline of most constituents of the fossil chironomid fauna. Perhaps there was some increase in environmental variability which interfered with the food supply for most chironomid taxa, especially perhaps for the taxa which are dependant on some form of primary production (e.g. the Orthocladiinae). Chironomus, because of its particular food source, was possibly removed from the effects.

Overall, the faunal composition in the period approached the present-day conditions in which Chironomus is clearly the dominant taxon, Polypedilum is present, Riethia is absent from benthic lake samples (but may be present in very low numbers thus avoiding detection), and Orthocladiinae are present but not abundant. Podonominae, whose fossils were probably stream-derived, might not have been found in present-day samples. But Tanytarsini, which were not recorded as fossils in the most recent sediments, are now living in the littoral zone, albeit in low numbers. The low abundances of Tanytarsini in the core and the present-day lake might be due to temperatures being generally too low for this taxon at this site. Tanypodinae, which were rare as fossils throughout the entire history of Blue Lake, appear to be more abundant in the present day fauna, especially the sub-dominant Procladius (Timms, 1980c; Table 9.2.) and Paramerina levidensis, which was found by the author in one benthic sample and in the hand-net samples.

9.4.6. Stratigraphies of the Less Common Fossil Chironomidae

The distribution of some of the less abundant fossil chironomid taxa will be discussed in the following section (see Fig. 9.5. and Table 9.5.). In the Chironomini three fossil taxa, Riethia, Polypedilum, and Chironomini A occurred almost continously throughout the Holocene, but were not common or present during the Pleistocene. The ecological requirements of Chironomini A are not known. As described earlier (see section 9.2.8.) this taxon might be the larvula of Chironomus.

The distribution of Polypedilum appears to be substrate dependant. In Lake St. Clair, this taxon was restricted to sandy substrates (Timms,

1978) and in Great Lake Polypedilum was most abundant at site NG3 (Fulton, 1983b) located in the recently flooded part of the lake. The substrate at this site was composed of sands with fine organic material. The only sandy substrates in Blue Lake are provided by the delta of the inflowing streams. But these areas might not be very stable due to changes in the velocity and volume of the inflows during the year. Furthermore fine organic material might not be deposited in these areas but transported further into the lake. These circumstances might have prevented this taxon from becoming more abundant in the fossil and present-day fauna of Blue Lake. The late appearance of Polypedilum at the end of the Pleistocene might be explained by the possibly reduced area of substrate available during that time as the inflows had just begun to deposit the deltaic areas.

Fossil remains of Riethia were never abundant in the samples from the core and living larvae have not been recorded from Blue Lake. Riethia spp. was clearly the dominant in several of the Tasmanian lakes studied, e.g. in Great Lake and Arthurs Lake (Fulton, 1983a,b), where Riethia was common or present at all sampling stations (including the stations with predominantly clay substrate) but was most abundant at the station with the highest amount of organic matter (NA1). Riethia was also dominant in Lakes St. Clair (where this taxon accounted for 50.6% of the total chironomid fauna) Dove (36.8% of the fauna), Dobson, Leake, and Tooms. In these lakes this taxon was generally associated with large amounts of organic matter in the sediments (Timms, 1978; percentage data calculated from Timms' abundance data). Riethia was abundant in Lake Tali Karng (9.8% of the fauna) where it mainly occurred in the littoral zone at the eastern end. The sediments of this part of the lake contained a great amount of woody detritus derived from the inlet (Timms, 1974). Therefore, Riethia appears to be adapted to a wide variety of substrates but prefers organically rich sediments, and can occur down to a water depth of 48 m (in Lake Dove; Timms, 1978) but highest numbers have been found in the littoral or littoriprofundal zone. Considering the distribution of this taxon in the above mentioned lakes the question arises why Riethia never became more abundant in Blue Lake as certainly the organically rich sediments are available in Blue Lake. It might be that water temperatures in Blue Lake are too low for this taxon and as most of the littoral area of Blue Lake is stony, it might not be able to live in this habitat,

where water temperatures during the summer might be sufficient for its development.

A similar reasoning might be applicable to the distribution of Procladius. The very low abundances of Procladius in the core samples might be due to some degree of under-representation of the fossil material. Head capsules of this genus are thin and apparently easily degraded (Walker et al., 1984). But even in the present-day fauna of Blue Lake Procladius occurs only in low numbers compared to the abundances of Chironomus. In Timms' study (1980c), Procladius larvae accounted for only 0.9% of the total fauna and in the author's study for 2.5% of all larvae found in the benthic samples. But in the Tasmanian lakes studied, Procladius was often the most abundant chironomid besides Riethia, e.g. in Lake St. Clair Procladius accounted for 31.2% of the fauna and in Lake Dove for 10.3% (Timms, 1978; percentage data calculated from Timms' abundance data) and in Lake Tali Karng Procladius (listed together with Ablabesmyia) accounted for 73.8% of the fauna (Timms, 1974; dito). Similar to Chironomus oppositus and Riethia, Procladius prefers detritus-laden mud (in Lake St. Clair, Timms, 1978; and in Lake Tali Karng, Timms, 1974) or organically rich sediments. In Arthurs Lake Procladius was most abundant at the sampling site containing the highest amount of organic matter (NA1; Fulton, 1983b). Therefore, food supply cannot be the restricting factor for the occurrence of Procladius in Blue Lake. This is even more so because Procladius is a facultative predator and does not have to rely necessarily on organic matter in the sediments. Thus, it appears that the relatively low temperatures in Blue Lake might be mainly responsible for the low occurrence of Procladius in Blue Lake. During the warmer period of the Holocene (sediment sequence III, see Appendix, Table IV.3.) Procladius did not appear to be more common than in the colder periods of the Holocene. But as this taxon might be under-represented in the fossil material, it might not be possible to gain reliable information about the development of populations of Procladius through time from fossil material.

9.4.7. Comparison of Blue Lake's Fossil Fauna with those from Lakes Grasmere and Monowai

Comparing the developmental history of Blue Lake with that of the last 6000 years of Lake Grasmere, it has been shown that the two lakes had a very different faunal composition. This was to be expected as the biogeographical links appear to be closest between Blue Lake and highland lakes in south-eastern Australia and Tasmania. The lower altitude of Lake Grasmere is reflected in the high proportions of Tanytarsini and Tanypodinae in its fossil fauna. But the most striking differences can be seen in the stratigraphies of the sediment parameters and their implications for the structure of the fossil fauna.

Low contents of water and organic matter in the sediments and a rapidly changing sedimentation regime occurred in Blue lake only during the Pleistocene. During this time fossil densities were low and the faunal composition unstable. With climatic amelioration and the subsequent vegetation cover of the catchment, input of minerogenous matter decreased and the proportion of organic matter in the sediments increased. A relatively stable sedimentation regime during most of the Holocene was the prerequisite for a comparatively stable structure of the fossil fauna in which changes occurred gradually without the abrupt disappearance and replacement of faunal elements.

During most of the last 6000 years of Lake Grasmere's history the organic matter content of the sediments resembled late-Pleistocene sediments. Furthermore, events like floods or earthquakes and a naturally high erosion rate in the Southern Alps did not provide a stable environment for the fauna for any length of time (the longest stable period lasted for approximately 1800 years and began ca. 3000 yr B.P.). These disturbances were clearly reflected in the succession of the fossil chironomid fauna. The fossil densities were strongly reduced by events which caused increased erosion, and abrupt changes in the faunal composition occurred (e.g. Corynocera disappeared from the fossil fauna before 1000 yr B.P.).

On a higher taxonomic level there were similarities between the fossil fauna of Lake Monowai, one of the deep cold lakes in the South Island

of New Zealand (45° 54′ South, 167° 25′ East), and that of Blue Lake. The fossil chironomid fauna in short sediment profiles (cored at a water depth of 160 m) from Lake Monowai was studied by Schakau (1986, and unpubl. data).

In the Lake Monowai fauna, Tanypodinae (nr. Pentaneura, and Tanypodinae sp. II, for description see Chapter VI) were rare and made up only 2.2% of the total fossils. Only Diamesinae fossils occurred with a lower relative abundance, 1.8% (Maoridiamesa, and nr. Limaya). In Blue Lake, living Diamesinae larvae or fossils were not found. As in Blue Lake, Tanytarsini occurred with a relatively low abundance of 5.3% in the fossil fauna from L. Monowai, with possibly three species in two genera (Tanytarsus spp., Stempellina). Orthocladiinae (51.5%) were the dominant element in the Lake Monowai fauna (as was found in Blue Lake) and also occurred with the highest species diversity (11 taxa). Except for taxa belonging to Eukiefferiella, Cricotopus, and Corynoneura, the orthoclad taxa in Lake Monowai belonged to species as yet undescribed, which was similar to the situation in Blue Lake. Chironomini in Lake Monowai were subdominant (22.5%) with the two most abundant taxa belonging to Chironomus and Paucispinigera (P. sp. a). The remaining Chironomini genera were Polypedilum, Chironomini sp. A, Riethia, and Harrisius. The generic composition of the Chironomini is very similar in the two lakes. The dominance pattern is also comparable: the two dominant taxa in both lakes were species of Chironomus, and two Orthocladiinae taxa (nr. Eukiefferiella in Blue Lake and Orthocladiinae sp. A, which I have placed tentatively near Rheocricotopus). The difference in the faunal composition of the two lakes was that the subdominant chironomid in Lake Monowai, endemic Paucispinigera sp. a, was nearly as abundant as Chironomus, whereas the dominance of Chironomus was very pronounced in the fossil fauna in Blue Lake (Table 9.4.).

9.4.8. Conclusion

To conclude, the succession of the fossil chironomid fauna from Blue Lake provided some information about the development of an alpine lake on mainland Australia during the last 13,000 years. The late-Pleistocene was characterized by low fossil densities and a low

species diversity, although most faunal elements colonized the lake during this period. The transition between the Pleistocene and Holocene showed the greatest magnitude of change in that both diversity and fossil numbers in the samples increased considerably and remained at maximum values throughout the early Holocene, which constituted the warmest period of the Holocene, when the lake might have had an increased autochthonous production. In the late Holocene, during which climatic conditions developed which were similar to the present, fossil densities and diversity declined, and then declined further in the youngest sediments which were deposited after 1700 yr B.P. The stratigraphy of the fossil chironomid fauna during the developmental history of Blue Lake showed a succession of cold-adapted forms to chironomid taxa which became more abundant, possibly through greater food supply combined with the effect of higher temperatures (in the early Holocene) and a return to more cold-adapted forms in the younger sediments.

Because the core does not cover the last 500-1000 years, it would be of interest to investigate the chironomid fauna of frozen finger cores (this coring method produces cores of the recently deposited sediments with a good chronological resolution of sediment parameters (Rymer & Neale, 1981)) to study the recent development of the fauna. These results could then be used for a comparison with the faunal succession of the core under study or could be used to determine whether the impact of European people on the alpine environment can be detected in the fossil chironomid fauna of Blue Lake.

The study of fossil chironomids from Blue Lake showed that there might be a detectable reaction of chironomids to climatic change. It appears that a possible warming might broaden the distribution of certain lowland taxa in terms of altitude (and restrict their distribution in the lowland areas) and might restrict the distribution of taxa which are adapted to a more limited range on the lower scale of the thermal regime. In the case of the fauna of high-altitude Australian lakes and streams, this restriction of more cold-adapted taxa might mean a continuous decline in abundance and possible extinction. Lowland taxa can move into higher altitude environments to escape higher temperatures, but there is no upwards movement possible in the Australian context for taxa already confined to higher altitude

environments. Blue Lake as a montane system has potential as a study site for the monitoring of the effects of climatic change because global warming might be amplified at high altitudes and might produce complex changes in cold-dominated systems. Aquatic insects as important constituents of any freshwater ecosystem will be affected as well and might even react more quickly to temperature changes than terrestrial vegetation (Walker et al., 1992). An aquatic system like Blue Lake could be monitored to detect changes in its aquatic fauna caused by changing climate. This could be done by using the above mentioned 'frozen finger cores'. Blue Lake is suitable for monitoring climatic change because anthropogenic impact on the lake was light in comparison with aquatic environments in more populated or accessible areas in the world. Effects measurable in aquatic systems which are due to anthropogenic stress might obscure the effects of changing climate (Melak, 1992).

This study has shown that much further work is necessary on the Chironomidae of Australia, especially those of alpine regions, with regard to taxonomy and ecology of the species present. More research is needed with regard to the factors which regulate the distribution of the species of Chironomidae.

Despite the lack of knowledge about many of the Chironomidae present in the fossil fauna of Blue Lake, this study has not only provided some information on how climatic change has possibly influenced the fossil chironomid fauna but has also provided baseline data from an alpine pristine environment with which the faunal composition and succession of other aquatic environments in Australia can be compared.

Summary

The stratigraphy of the fossil Chironomidae from Blue Lake, Mt. Kosciusko National Park, Australia, is presented. The 4.42 m long core studied provides a record of the fossil fauna from the initial filling phase of the lake (ca. 13,000 yr B.P.) to approximately 500-1000 yr B.P. The fossil chironomid fauna was dominated by Orthocladiinae and Chironomini. A relatively high proportion of Podonominae remains occurred, indicative of the alpine environment of the study site.

Tanytarsini and Tanypodinae head capsules were rare throughout the entire period studied. The fossil fauna comprised 28 taxa, but was dominated by Podonomus in the late-Pleistocene sediments, by nr. Eukiefferiella in the early Holocene and by Chironomus in the younger sediments. A correspondence analysis identified three groups of sediment sequences and excluded nearly all Pleistocene samples. The late-Pleistocene period was characterized by low numbers of chironomid remains and a rapidly changing faunal composition reflecting the cold and sedimentary unstable conditions of this period. Climatic amelioration at the beginning of the Holocene was indicated by an increase in organic matter in the sediments, and higher numbers of chironomid remains in the samples. The three sediment sequences derived from the correspondence analysis could be correlated with the main climatic periods of the Holocene. It is suggested that temperature changes may have been mainly responsible for the changes in the composition of the fossil chironomid fauna. An additional important factor may have been the substrate.

CHAPTER X

GENERAL DISCUSSION

In this thesis a multiparameter approach to the study of sediments was used to elucidate past conditions of a small lake and its catchment in the high country of the South Island of New Zealand. The sediment core collected from Lake Grasmere covered the sediment record of the last 6000 years of the lake's history.

The lake has been dammed by ice-eroded rock and three alluvial fans (see Chapter III) and Gage (1959) suggested that it came into existence at some time after the ice retreat 13,000 years ago. The basal layer of the core was composed of clay and silt preventing the coring tube from penetrating the sediment further. There is the possibility that the site of the coring was dry prior to ca. 6000 yr B.P. and that the sedimentary record contained in the core covered the entire lacustrine phase of the lake. After 7000 yr B.P. the climate in New Zealand became cooler and wetter overall, and by 3000 yr B.P. colder climates with drier summers and relatively variable conditions were established (McGlone et al., 1992). With overall wetter conditions and a possibly declining evaporation rate previously dry basins might have filled with water. This situation was found for some lakes in Central Alberta (Forbes & Hickman, 1981; Hickman, 1987), but so far there is no evidence for the formation of lakes due to climatic change in New Zealand about 6000 yr B.P. Lake Maratoto, North Island, has been in existence since approximately 17,000 yr B.P., and albeit shallow was never dry during its history (Boubee, 1983).

If the lake filled 6000 years ago, the origin of the basal clay/silt layer has to be established. This layer corresponds visually to glacial till. Forbes & Hickman (1981), who found a similar clay layer at the bottom of cores from two lakes in Central Alberta, suggested that the organic deposits built up during the dry phase might have been eroded away by aeolian activity before the basin became a lake. This is unlikely for Lake Grasmere as its catchment was forested before 6000 yr B.P. (Molloy, 1977). They also suggested that the clays might represent rapid redeposition resulting from shoreline erosion as

the lake filled. But shoreline erosion results more often in the deposition of sand in the deeper parts of the lake (Davis et al., 1985) and the basal layer in the Lake Grasmere core did not contain particles larger than silt (Troels-Smith, 1955). The particle size and the absence of sand indicate that the basal layer of the Lake Grasmere core was probably deposited under aquatic conditions. A further indication of aquatic deposition was the presence of aquatic microfossils in the upper horizon (322 cm) of the clay/silt layer. These sediments might have been deposited as a result of a high magnitude storm (or storms) which caused high sediment loads in an inflowing river. For example, in Lake Tutira, North Island, Cyclone Bola produced an inorganic sediment layer of an average thickness of 36 cm. This is an extremely high sediment accumulation after one storm but was partly aggravated by anthropogenic activities in the catchment (Ryan, 1992). The South Island is a region of frequent natural erosion (McSaveney & Whitehouse, 1989), where a major rainstorm (or a series of storms) could be responsible for the amount of clays and silt deposited in the basal layer of the core, even before the advent of human-induced erosion (Grant, 1989). For these reasons I suggest that Lake Grasmere has been in existence for a longer period than was recovered in the core.

The river flowing into Lake Grasmere 6000 years ago could have been the Cass River which in the past had migrated across the floor of the Cass Basin (Burrows, 1983). It might even be possible that the river only temporarily changed its course. As can be seen in the aerial photograph of Lake Grasmere and its catchment (Plate 2.1.), it is conceivable that the Cass River could change its course during a large flood, break through between Little Bailey and Romulus Hill and then flow towards Lake Grasmere.

Fig. 10.1. is a summary of the successions of several parameters studied in the Lake Grasmere core. These include the radiocarbon dates for three sediment layers, the profile for loss-on-ignition, the pollen zones and the changes of the water level in the lake as inferred from changes in the composition of the fossil diatom flora in the core, and the faunal zonation of the fossil Chironomidae and Cladocera.

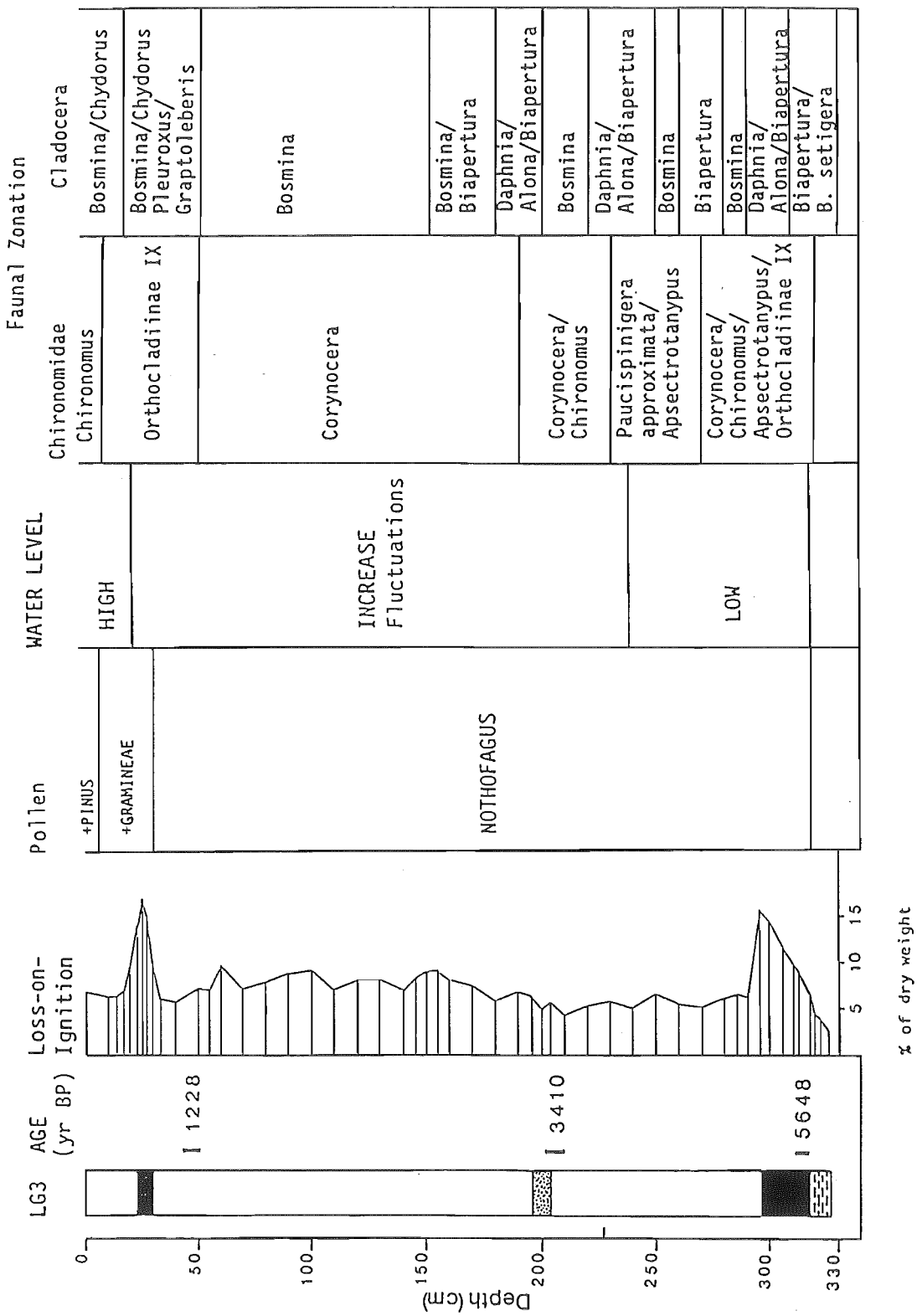


Fig. 10.1. Summary figure illustrating major features of the Lake Grasmere core: the age of the sediments, the profile of loss-on-ignition in the core, the results of the pollen analysis , the past water level as inferred from the fossil diatom stratigraphy, and the faunal zonation of fossil Chironomidae and Cladocera (Biapertura is B. affinis, Alona is A. quadrangularis). Lithological symbols: ▩ - clay/silt, □ - clay gyttja, ▮ - organic content >10%, ▦ - grana minora.

The historical record is divided into 10 sediment zones for convenience in discussion (Table 10.1.). The designation of the zones is subjective and is based on the changes in sediment regime which are reflected by at least one of the other parameters studied.

In correlating the stratigraphies of the different sediment parameters studied (organic matter content, fossil diatoms, Chironomidae, Cladocera, and plant pigments) it can be shown that Lake Grasmere was strongly influenced by the geologically active and variable environment of the Southern Alps. During the last 6000 years, allochthonous input was relatively high, but environmental disturbances of different degrees of magnitude caused pulses of increased amounts of mineral matter input. Five such events were recognized in the core, including the basal clay/silt layer. Alternating with these events were relatively stable periods of differing durations and varying lake productivity (see Table 10.1.)

Zone 10 encompassed the basal clay/silt layer which did not contain any microfossils in its lowermost horizon. Low pigment concentrations (chlorophyll derivatives and total carotenoids) and a high chlorophyll derivatives:total carotenoids ratio pointed to a partly terrestrial source of the deposited material. The high input of fine sediments into the lake appears to have been catastrophic for the lake biota and might have initially obliterated the fauna, e.g. through physical burial or interference with the food available. Warwick (1980) also found that increased amounts of mineral sedimentation in the Bay of Quinte, Ontario, influenced the chironomid communities directly and were partly responsible for the decline in species numbers and abundance of the individual species.

In the 322 cm horizon, close to the top of the clay/silt layer, very low numbers of biological remains were found. Clearing of the lake waters either took some time, inhibiting the lake biota, or the number of remains was diluted by the high sedimentation rate.

Table 10.1. The zonation of the sediments in the core.

Zone 1: 10 cm - top of the core
Zone 2: 17 cm - 12 cm (increased mineral input)
Zone 3: 27 cm - 20 cm (higher productivity)
Zone 4: 55 cm - 33 cm (increased mineral input)
Zone 5: 195 cm - 60 cm (stable, higher productivity)
Zone 6: 210 cm - 196 cm (increased mineral input)
Zone 7: 250 cm - 220 cm (stable, low productivity)
Zone 8: 290 cm - 260 cm (low productivity, increasing mineral input)
Zone 9: 319 cm - 295 cm (higher productivity)
Zone 10: 326 cm - 320 cm (increased mineral input).

A colour change of the sediments above the 320 cm horizon marked the beginning of zone 9. The content of organic matter increased to its first maximum in the core which, in conjunction with relatively high concentrations of both pigment types, pointed to a higher lake productivity (than during subsequent periods) in this zone. The abrupt decline of these parameters above 295 cm indicated that this increase in lake productivity was only temporary, possibly caused by nutrients carried into the lake absorbed to the clay particles of zone 10. High proportions of small Fragilaria species in zone 9 indicated a shallow lake (3-5 m deep) with extensive macrophyte beds. Macrophyte stands were probably not very dense because Corynocera, which inhabits flocculent sediments, was amongst the dominant species in the chironomid fauna. In this zone, the fossil chironomids occurred with their highest species diversity, and with relatively large numbers of remains. In the Cladocera fauna, littoral chydorids dominated (Biapertura affinis and Alona quadrangularis) which also indicated low lake levels and a extensive growth of macrophytes.

In zone 8, a paling of the sediments concurrent with a decline in organic matter content indicated a return to less productive conditions in the lake. Input of minerogenous matter appeared to have increased at the 270 cm horizon and culminated in the deposition of a dark grey layer between 260 and 258 cm. The number of fossils (diatoms, Chironomidae and Cladocera) also declined to a minimum between 270 and 260 cm. The low concentration of total carotenoids

caused high chlorophyll derivatives:total carotenoid ratios which increased throughout the zone pointing to allochthonous input. The proportions of Fragilaria and Biapertura affinis were still relatively high so that macrophytes must have persisted throughout this zone (a proportion of macrophytes was indicated in most zones in the core). The abundance of Corynocera declined possibly because of interference with the substrate of its habitat. Paucispinigera approximata, a chironomid common in freshwater systems with Nothofagus forest in the catchment, became dominant during this period. This taxon might have been less influenced by the mineral sedimentation as its food source is possibly Nothofagus litter entering the lake.

In zone 7, the organic matter content remained relatively low, and the concentrations of fossil pigments increased slightly. Lake productivity was probably low during this period. The composition of the diatom flora changed and the facultative plankter Cyclotella stelligera occurred as a greater proportion in the flora. In the Cladocera fauna, Bosmina meridionalis, became more abundant. These changes might indicate a progressive rise of the lake level from the 240 cm horizon upwards. Paucispinigera approximata disappeared from the fossil fauna in this zone, which might have been caused by a reduction in its food matter. Fire, which has been part of the ecological regime in the South Island (Molloy, 1977), could have destroyed part of the Nothofagus forest surrounding the lake.

The following sediments, zone 6, contained the layer in which Grana minora particles were deposited. The organic matter content of the sediments in this zone decreased only slightly but the proportion of water was very low indicating compacted sediments. The ratio of chlorophyll derivatives:total carotenoids was unusually high which again pointed to a terrestrial origin of the organic matter in this zone. The deposition of sand particles in the deeper part of the lake might have been due to redeposition of littoral sediments through a high magnitude storm or due to a landslide caused by an earthquake. The fossil densities and the number of taxa in the Chironomidae and Cladocera were very low in this zone. The composition of the fossil faunas changed and littoral taxa accounted for a larger proportion of the fauna, e.g. Paratanytarsus and Alona quadrangularis.

In the sediments above the Grana minora layer (zone 5) the lake biota recovered from the impact of the high mineral accumulation in the previous zone and all sedimentary parameters studied increased considerably and remained high from 160 to 60 cm in the core. The organic matter content in the sediments of zone 5 was 2.5% higher than in the older sediments, and the concentration of the fossil pigments was relatively high indicative of an increased lake productivity during this time. The lake level was higher than during the initial shallow phase but might have fluctuated as was shown by the alternating dominance of Fragilaria species and Cyclotella stelligera. The five-fold increase of Cladocera remains at the 150 cm horizon was mainly due to a greater proportion of Bosmina also indicating higher lake productivity and a high lake level. The fluctuations in the relative abundances of the dominant fossil diatoms could also be recognized in the profile of the relative abundance of Bosmina in this zone. Corynocera was the dominant chironomid during this period occurring in large numbers and indicating high transparency of the lake waters and flocculent sediments, which possibly contained a relatively large proportion of benthic algae. The high concentration of fossil pigments in the sediments was probably partly due to good preservation of pigments caused by rapid burial of benthic algae by mineral sedimentation, which was still relatively high in this zone as shown by the small increase in the organic matter content. Zone 5 constituted the longest stable period in the recorded past of Lake Grasmere lasting from approximately 3000 yr B.P. to 1500 yr B.P. (extrapolated from the existing radiocarbon dates).

Marked changes in the conditions of the lake occurred in zone 4. The organic matter content declined but did not reach levels as low as in the older sediments of zone 8 and 7. The water content also decreased indicating more compact sediments and an increase of the amount of minerogenous input. Although the concentrations of both pigment types were lower, the pigment ratio was not as high as in zones 10, 8, and 6, which could mean possibly a lower proportion of terrestrial organic material input than was prevalent in the older sediments. The number of diatoms declined to a minimum in the 35 cm sample and fossil densities of Chironomidae and Cladocera were extremely low in the 40 cm sample, (e.g. 2 head capsules). The relative abundance of Cyclotella stelligera was high, pointing to a higher lake level. This

suggestion was not strongly corroborated by the composition of the fossil Cladocera fauna. The proportion of Bosmina decreased, which could have been due to the increased mineral input, and therefore does not necessarily indicate a change in water level. In this zone littoral Chydoridae became more abundant. Also the dominance pattern amongst the Chydoridae changed. Alona quadrangularis and Biapertura affinis, which were the dominant Chydoridae in the older zones, became less abundant and the relative abundances of Graptoleberis testudinaria, Chydorus sp. and Pleuroxus hastirostris increased. As all these five chydorid taxa live amongst macrophytes it is not known what had caused the change in the faunal structure. There must have been alterations in the bottom habitat because Corynocera, which appears to be dependant on a specific substrate type, and had been dominant, was not found above the 50 cm horizon. Above that level, Orthocladiinae sp. IX became the dominant chironomid taxon. The nature of the event which caused the decline in fossil densities and some of the changes in the lake biota is not known. There is the possibility that the New Ribbonwood Fan (Fig. 2.1.; the fan can be seen at the far end of Lake Grasmere in Plate 2.1.) was expanding and began to encroach onto the lake causing a change in the lake area. Gage (1959) suggested that the lake had extended further eastwards covering the area which is now the New Ribbonwood Fan. This fan is the youngest of the three alluvial fans bordering the lake and was still active in historic times (Gage, 1959).

The following sediment layer, zone 3, was probably deposited after the arrival of the Polynesian people as indicated by the presence of grass pollen above the 30 cm level. Lake productivity was relatively high in this zone as was shown by the maximum content of organic matter in the core, increased pigment concentrations and diatom numbers, and also high fossil densities of Chironomidae and Cladocera. The proportion of Fragilaria increased in this zone and that of Bosmina was relatively low, indicating a possible temporary lowering of the lake level. The highest numbers of Orthocladiinae sp. IX, and of Pleuroxus hastirostris, and high numbers of Chydorus, occurred in this zone pointing to extensive macrophyte growth in the lake during this period. The nutrient input into the lake was possibly caused by burning of the catchment vegetation by the Polynesian people.

Increased mineral sediment accumulation was again indicated in zone 2 (possibly due to increased erosion from the catchment after the Polynesian fires), in which the organic matter content declined to values similar to those in zone 4. Pigment concentrations and fossil densities were also less. The relative abundance of Orthocladiinae sp. IX declined and Chironomus became more abundant. In the fossil Chydoridae only Chydorus occurred with a relatively high abundance. The proportions of Bosmina and Cyclotella stelligera were very high indicating a return to deeper water conditions.

In the youngest sediments, zone 1, the lake productivity increased again as shown by higher pigment concentrations, especially those of total carotenoids, and an increase of fossil densities of diatoms and Cladocera, and to a lesser extent of fossil Chironomidae. The uppermost 6 cm of this zone were deposited after the arrival of the European settlers as shown by the presence of Pinus pollen in the sediments. Chironomus and in the Chydoridae, Chydorus, were the dominant faunal components. Both species can occur in abundance in more eutrophic lakes and their increased proportion in the top sediments might indicate changed trophic conditions in the lake as a result of the activities of the European settlers. But even with a possible increase in the productivity of the lake, the low organic matter content of the sediments in this zone indicated that the mineral sediment accumulation remained relatively large during this period, possibly caused by human-induced erosion (McSaveney & Whitehouse, 1989). The appearance of Diatoma elongatum in the top sediments might point to a rise of the water level to its present depth in this zone (possibly caused by further damming of the lake by the New Ribbonwood Fan).

In conclusion, the stratigraphies of the different parameters studied showed a good correlation, which served as a control for the interpretation of the individual parameters. The multiparameter approach increased the representativeness of the results as only a single core from the lake could be investigated. However, Davis et al. (1985) studying a number of cores collected in Mirror Lake, New Hampshire, found that the sediments in the different cores were nearly uniform in composition so that changes and proportions of the different sediment constituents of the central core should be typical

of the conditions in the central basin of the lake. Closer sampling intervals would have provided a finer resolution of the changes in the lake but this had to be restricted because of time and financial restraints. For future research it would be interesting to study a core which covers the entire history of the lake to be able to study the changes in the lake biota during the late-Pleistocene and early Holocene, as well as the most recent sediments (e.g. a frozen finger core). This would provide more complete baseline data against which the on-going development of Lake Grasmere can be monitored. This study has provided also information about the distribution and some aspects of the ecology of the Chironomidae and Cladocera in the South Island of New Zealand, but it has also shown that more research is needed on the taxonomy and ecology of these groups.

Studying chironomid remains from surficial sediments from different lakes in the South Island has proven useful in two respects: the faunal structure of the Chironomidae in several of the lakes could be related to certain limnological conditions; and some of the fossil assemblages in the surficial sediment samples could be used as analogues for fossil communities in the core.

The fossil Chironomidae from Lake Grasmere differed markedly from that in Blue Lake. The succession of the fossil fauna in Lake Grasmere was characterized by pronounced fluctuations in species numbers and abundance, and abrupt changes in the composition of the fauna. A similar pattern of community changes was restricted in Blue Lake to the part of the core deposited during the late-Pleistocene, whereas changes in the proportions of taxa in the fossil fauna occurred gradually during the Holocene in Blue Lake.

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APPENDIX I

LIST OF PHOTOPLATES

Plate I. Longitudinal View of Halved Sediment Core from Lake Grasmere in Sampling PVC - Tubing.

Fig. I - Fig. III. Blue Lake, Australia: Fossil Chironomid Head Capsules.

Fig. IV - Fig. V. Lake Monowai: Fossil Chironomid Head Capsules.

Fig. VI - Fig. IX. Lake Grasmere: Fossil and Recent Chironomid Head Capsules.

Fig. X. Lake Grasmere: Fossil Cladocera.

Fig. XI - Fig. XVI. Lake Grasmere: Fossil Chydoridae.

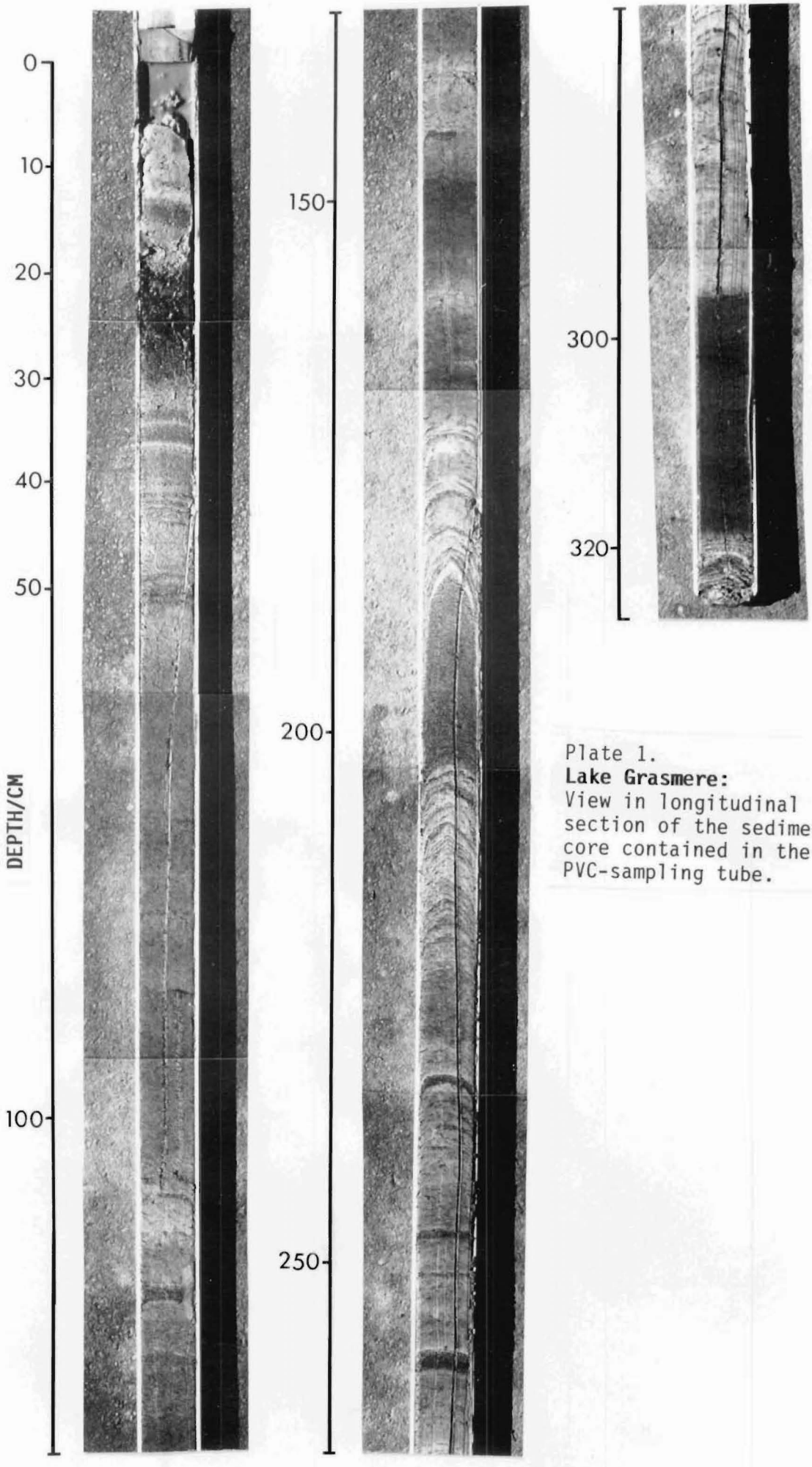
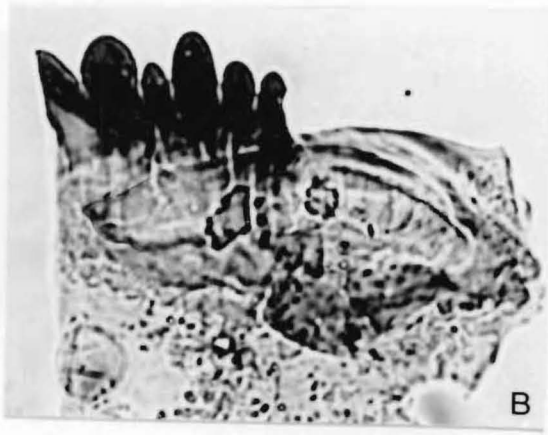
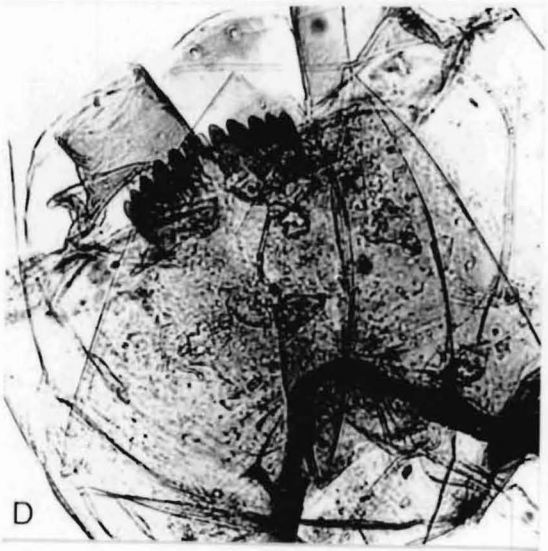
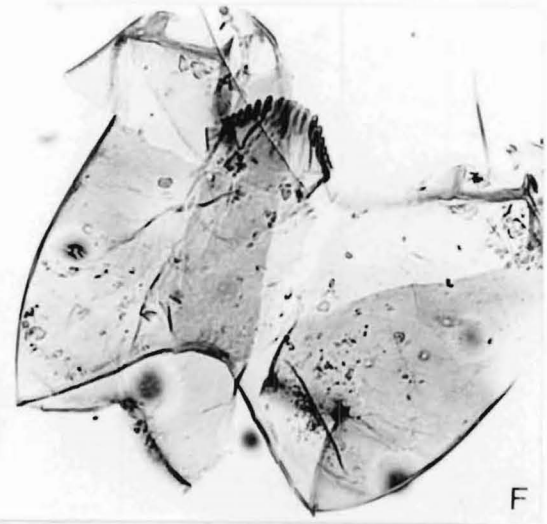
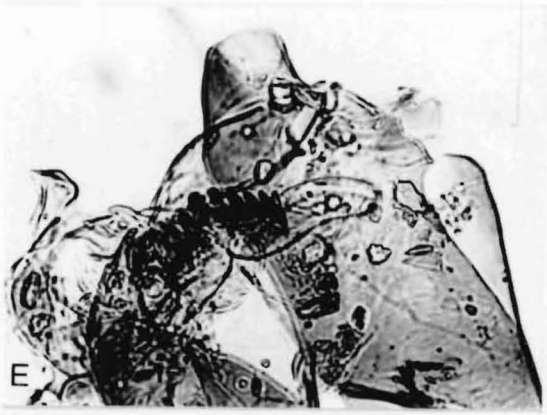


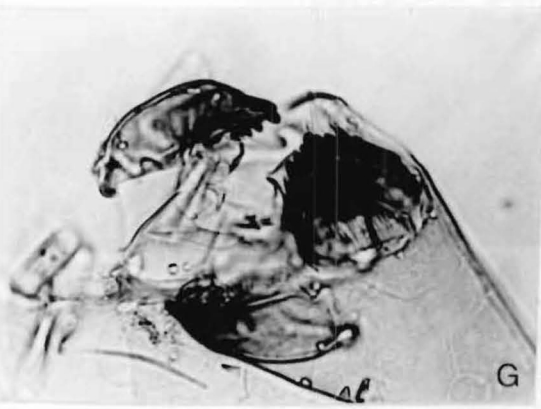
Plate 1.
Lake Grasmere:
View in longitudinal section of the sediment core contained in the PVC-sampling tube.











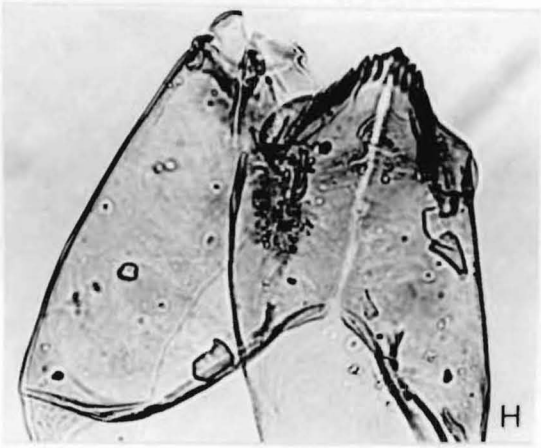
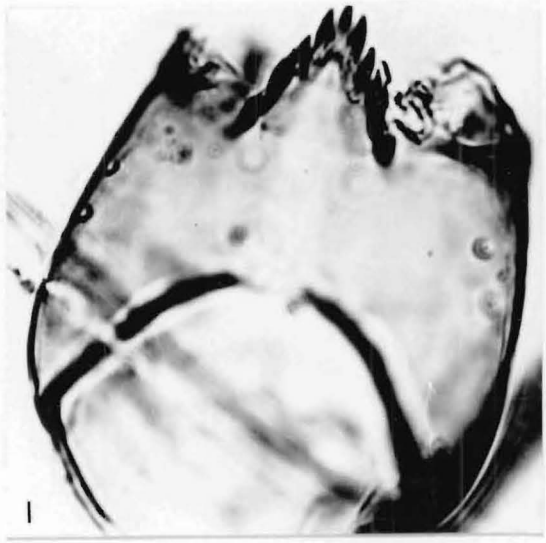
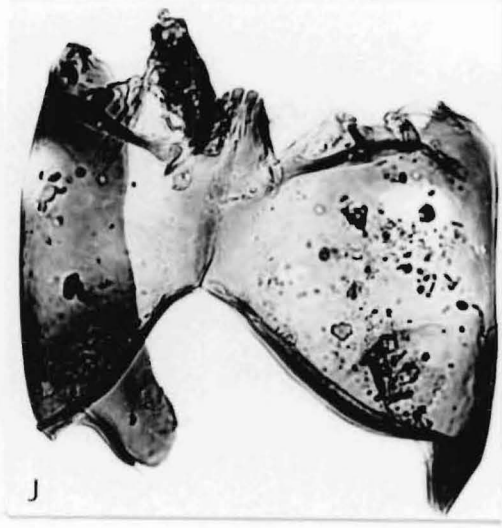
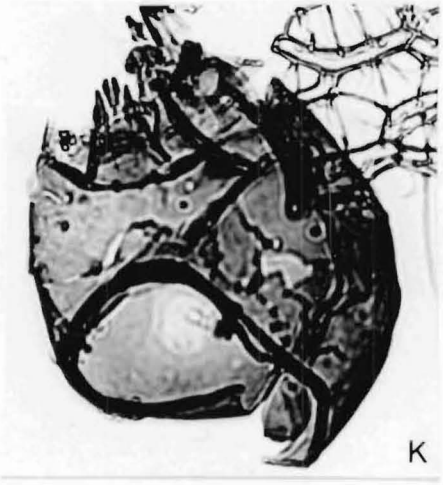
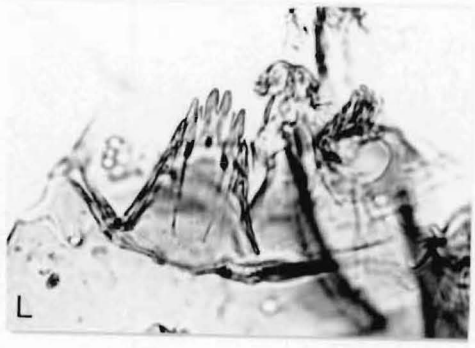


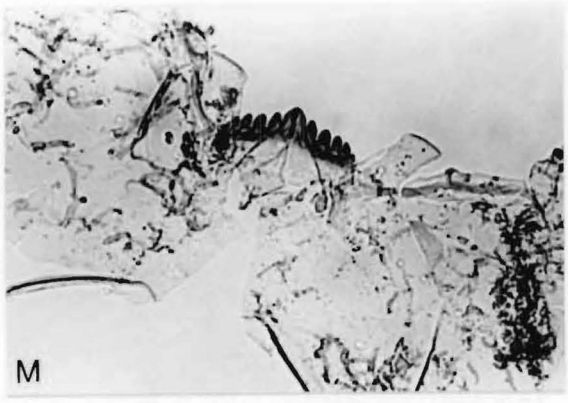
Fig. I.

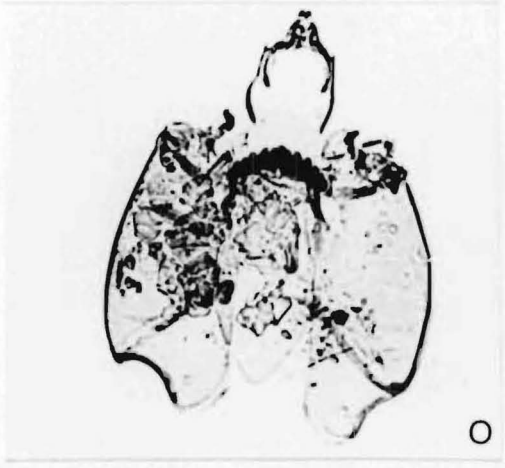












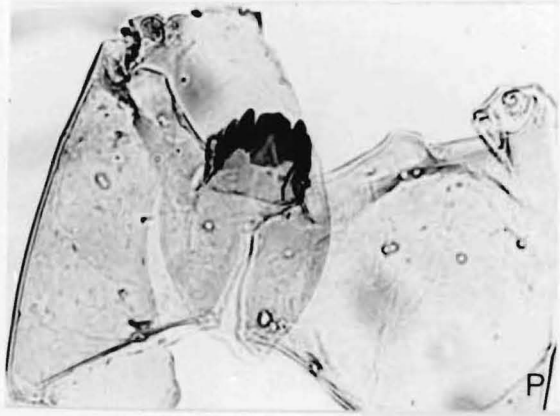
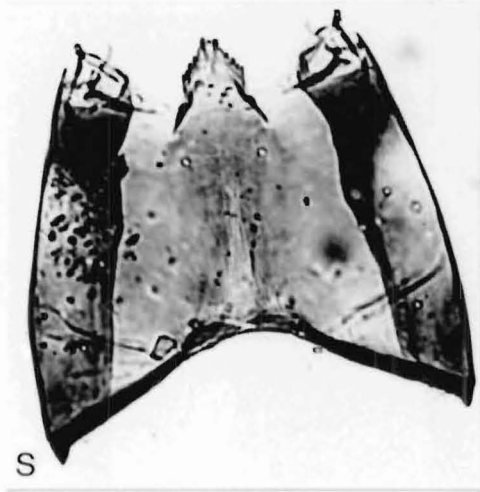


Fig. II.

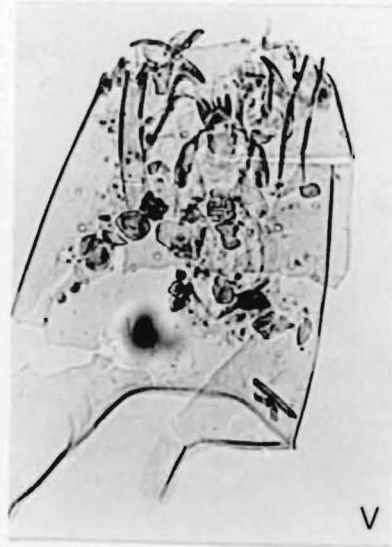


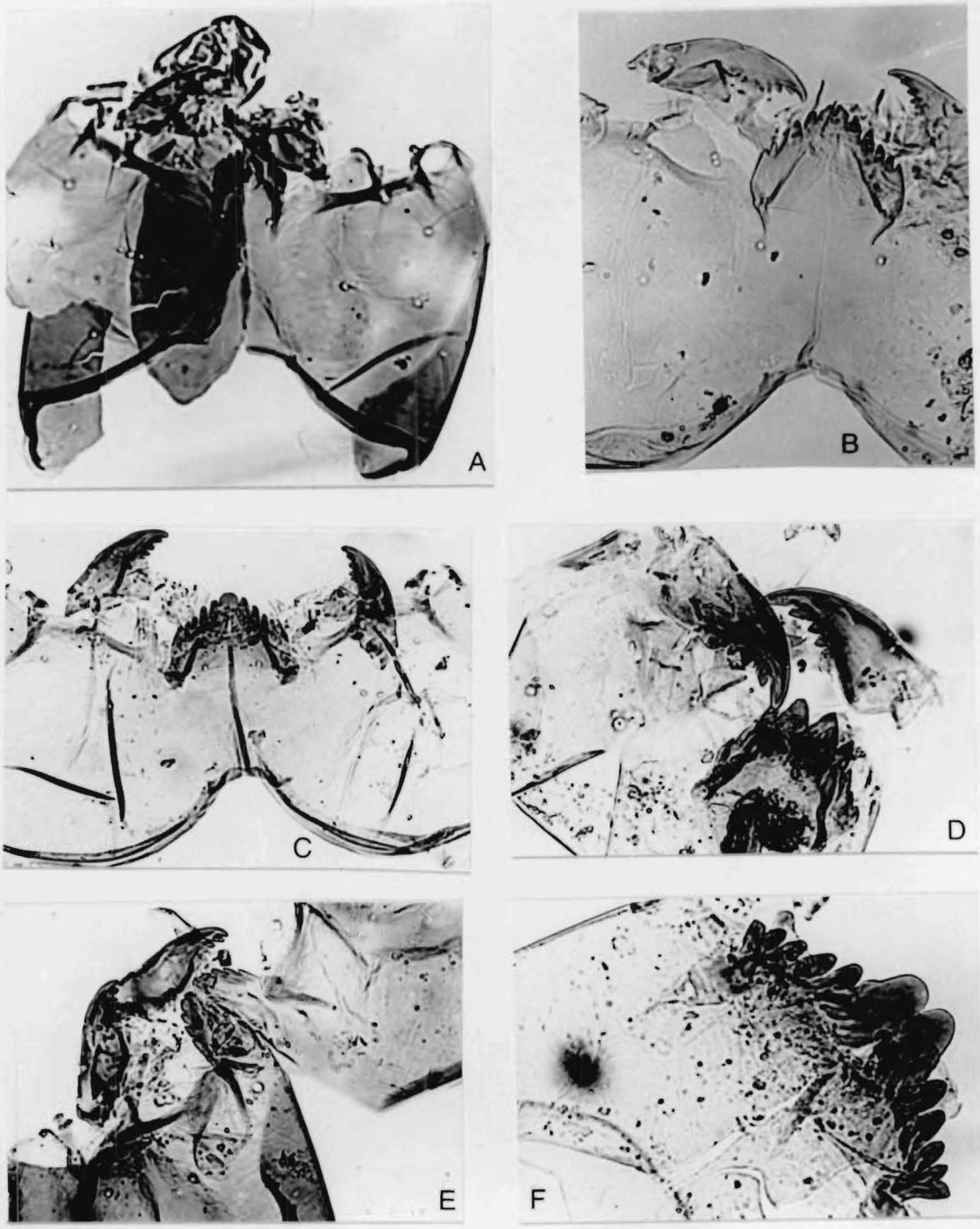
Blue Lake: Fossil Chironomid Head Capsules of Selected Taxa.

Fig. I. A: Chironomini sp. A, x 430;
B: *Riethia*, x 500;
C: *Xenochironomus*, x 500;
D: *Tanytarsus*, x 209;
E: Tanytarsini sp. I, x 380;
F: *Podonomus*, x 450;
G: *Parochlus*, x 385;
H: Prodiamesinae (?), x 335.

Fig.II.
I: Orthocladiinae sp. XIII, x 600;
J: Orthocladiinae sp. X, x 390;
K: Orthocladiinae sp. XII, x 330;
L: Orthocladiinae sp. XII, x 500;
M: Orthocladiinae sp. 14, x 335;
N: *Eukiefferiella claripennis* gr., x 380;
O: Orthocladiinae sp. I, x 250;
P: Orthocladiinae sp. IV, x 380.

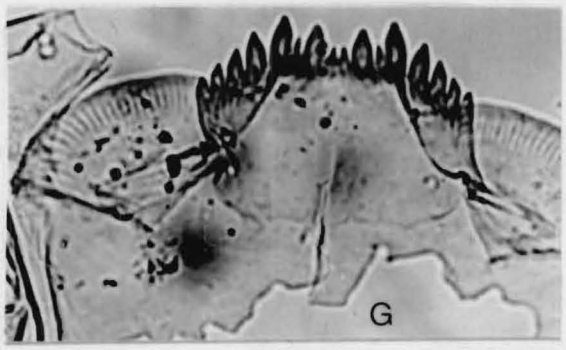
Fig. III.
Q: Orthocladiinae sp. III, x 400;
R: nr. *Eukiefferiella*, x 320;
S: *Corynoneura*, x 500;
T: Orthocladiinae sp. V, x 300;
U: Tanypodinae sp. I, x 430;
V: *Paramerina levidensis*, x 385.

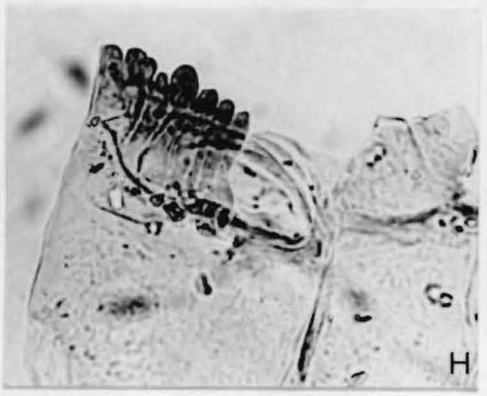




Lake Monowai: Fossil Chironomid Head Capsules of Selected Taxa.

Fig. IV.
A: Orthocladiinae sp. 2, x 450;
B: *Eukiefferiella*, x 390;
C: Orthocladiinae sp. 14, x 250;
D: Orthocladiinae sp. V, x 325;
E: Orthocladiinae sp. 13, x 295;
F: Orthocladiinae sp. 9, x 300.





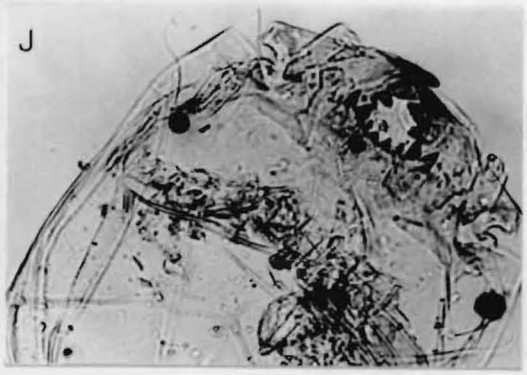
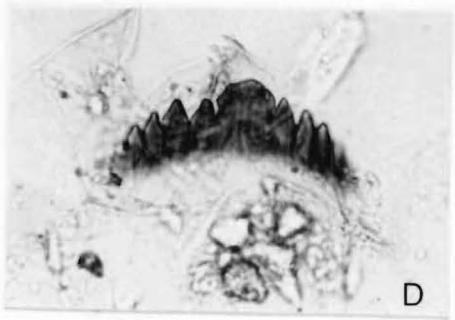
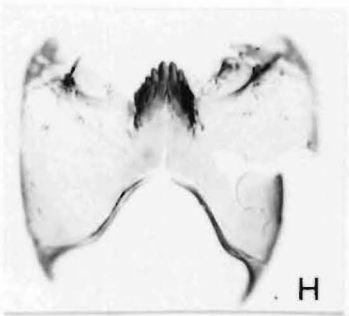
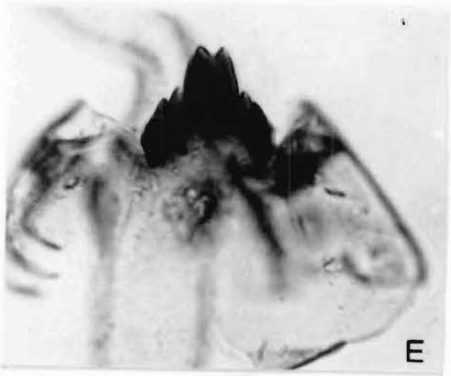


Fig. V.
G: *Paucispinigera* sp. a, x 410;
H: *Riethia*, x 330;
I: *Stempellina*, x 235;
J: *Harrisius* (?), x 310;
K: nr. *Limaya*, x 335;
L: *Parochlus*, x 310;
M: *Maoridiamesa*, x 310.







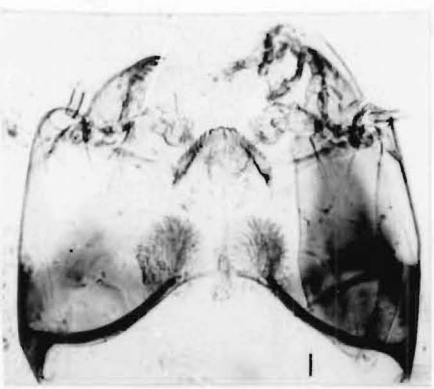


Fig. VI. Fossil Chironomid Head Capsules of Selected Taxa

Lake Grasmere:

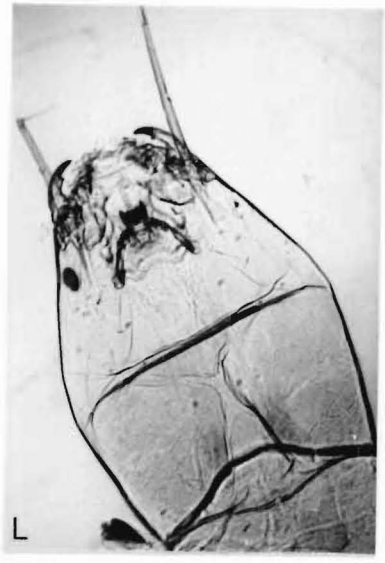
A: *Cricotopus*, x 338;
B: *Cricotopus* sp. 25, x 390;
C: *Matakiri*, x 275;
D: Orthocladiinae sp. I, x 388;
E: nr. *Synorthocladius*, x 600;
F: Orthocladiinae sp. XV, x 557;
G: *Eukiefferiella*, x 600;

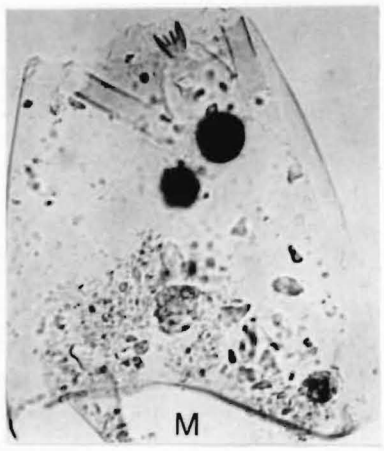
Lady Lake:

H: Heptagyini sp. I, x 136;

Bridge Farm (9/12/90):

I: Heptagyini sp. II, x 94.





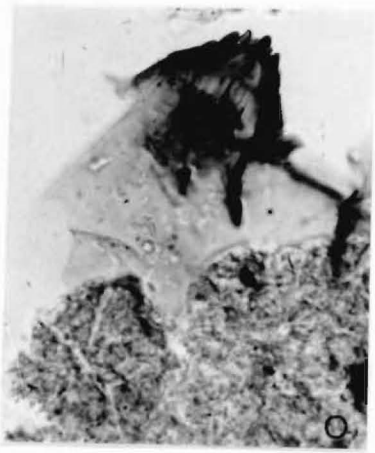
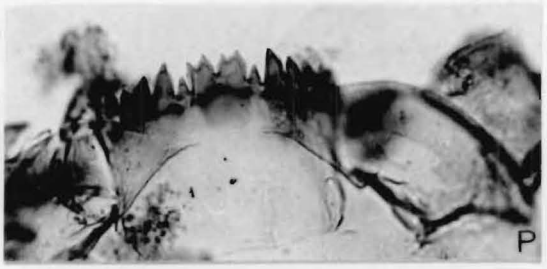
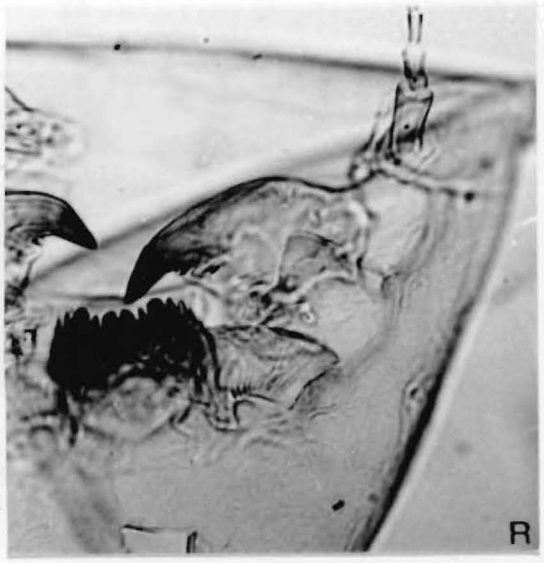
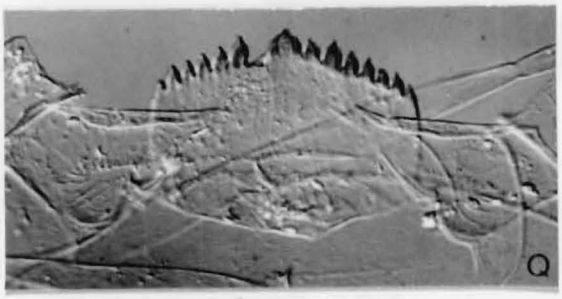


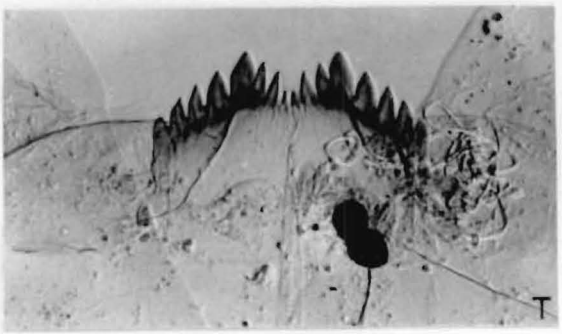
Fig. VII. Chironomid Head Capsules of Selected Taxa

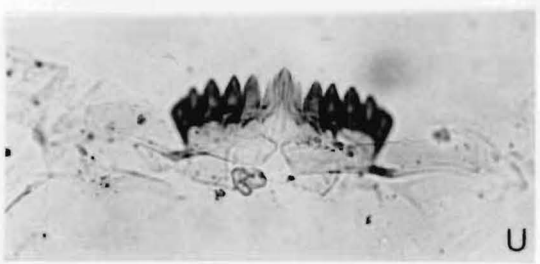
Lake Matheson: J : nr. *Psectrotanypus*, x 447;
Lake Grasmere: K : *Apsectrotanypus*, x 110;
L: nr. *Pentaneura*, x 58;
M: Tanypodinae sp. I, x 400;
N: *Gressittius antarcticus*, x 445;
O: *Parochlus*, x 485.

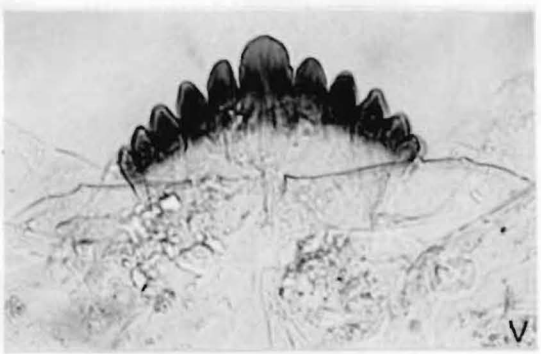












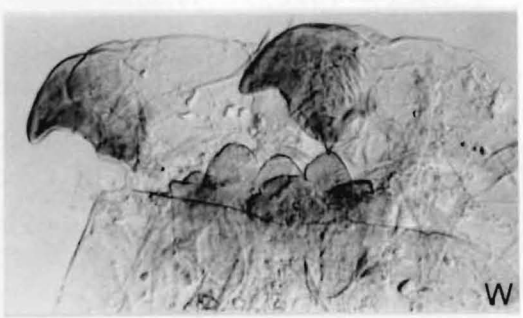
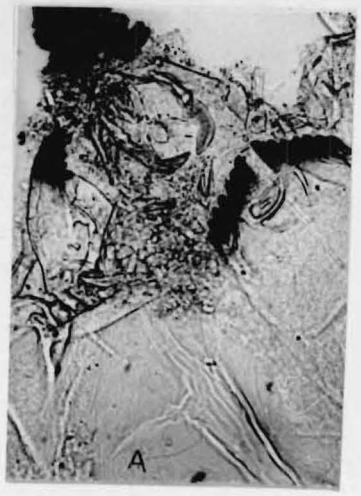
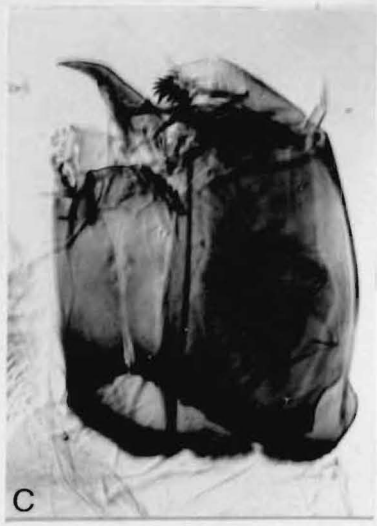


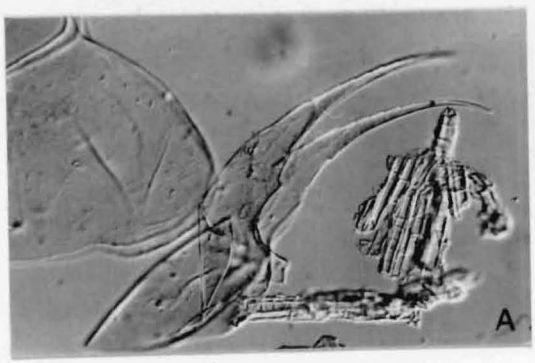
Fig. VIII.

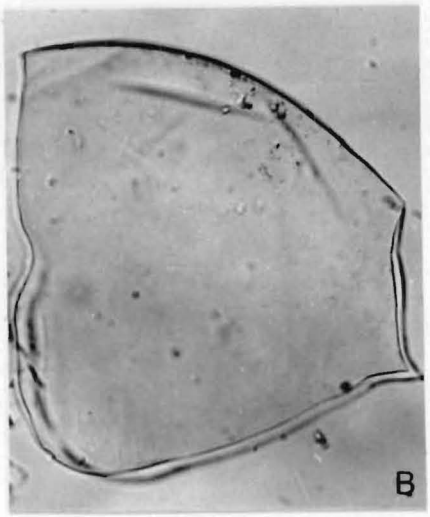


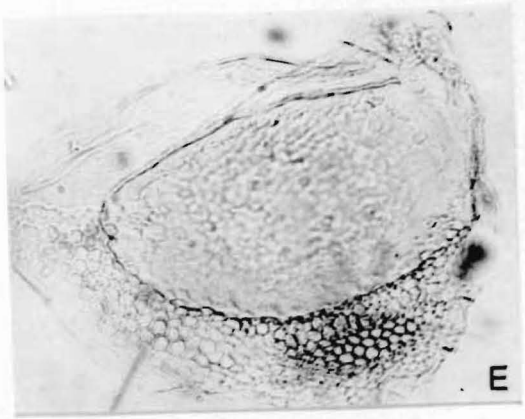


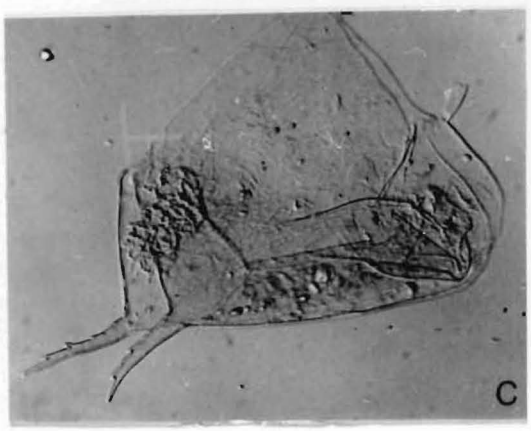
Lake Grasmere: Fossil and Recent Chironomid Head Capsules of Selected Taxa.
Fig. IX.
A: *Cricotopus*, x 207;
B: Orthocladiinae sp. C, x 165;
C: Heptagyini sp. III, x 510 (Cass)
D: Orthocladiinae sp. IX, x 325;
E: Orthocladiinae sp. V, x 300 (Cass).

Fig. VIII.
P: *Polypedilum*, x 300;
Q: *Parachironomus*, x 220;
R: *Xenochironomus*, x 485;
S: *Cryptochironomus*, x 430;
T: *Paucispinigera approximata*, x 355;
U: *Tanytarsus funebris*, x 300;
V: *Paratanytarsus*, x 415;
W: *Corynocera*, x 350;
X: *Corynocera*, x 400.









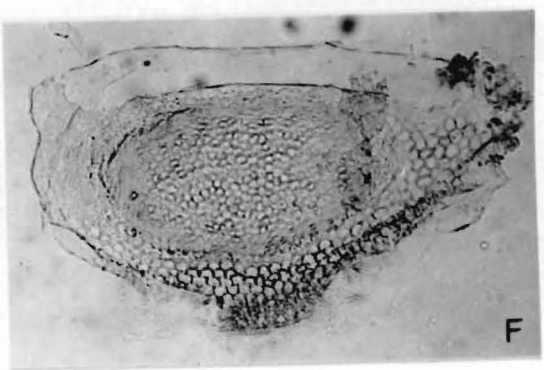
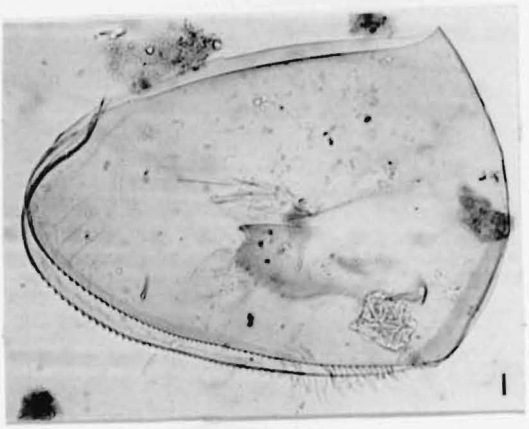
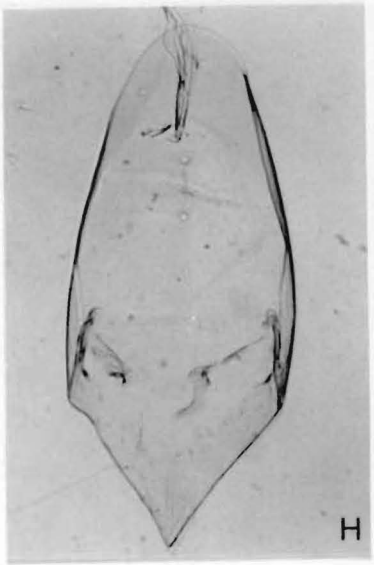
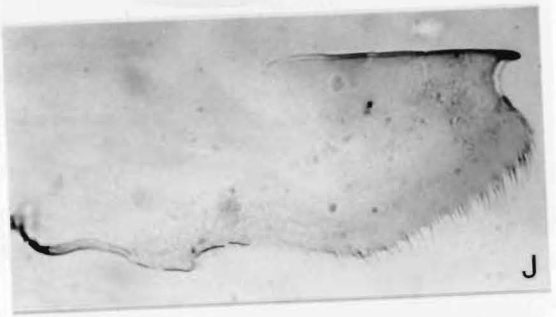
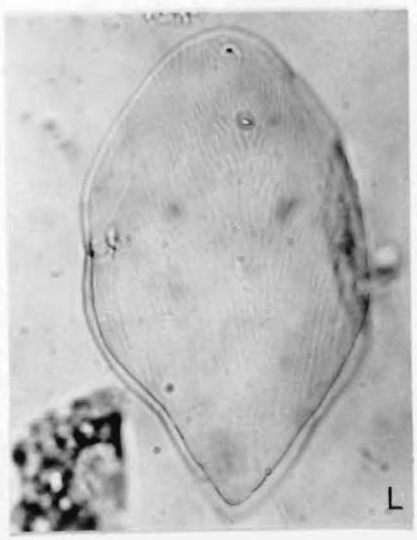


Fig. X. **Lake Grasmere:**
Fossil Cladocera
Bosmina meriodinalis;
A: Headshield, x 90;
B: Carapace, with short mucrones, x 210;
C: Carapace, with long mucrones, x 190;
Daphnia sp.
D: Ephippium, x 90;
Simocephalus sp.
E: Ephippium, x 180;
F: Ephippium, x 150.









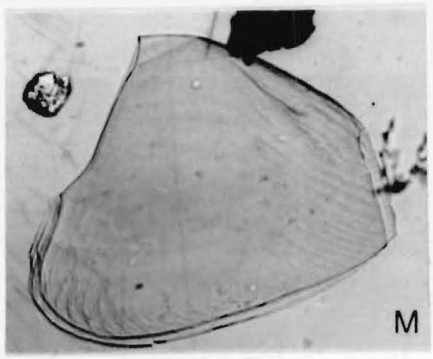
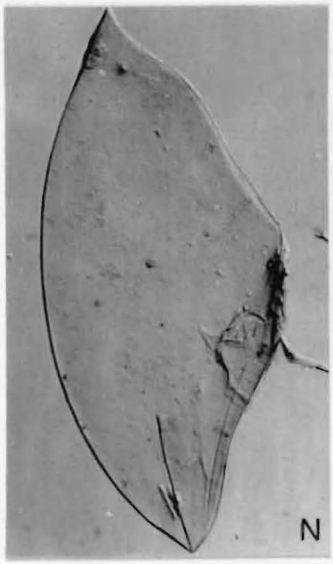
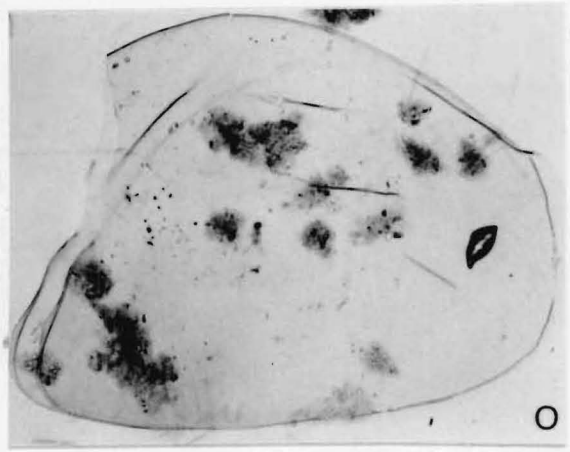
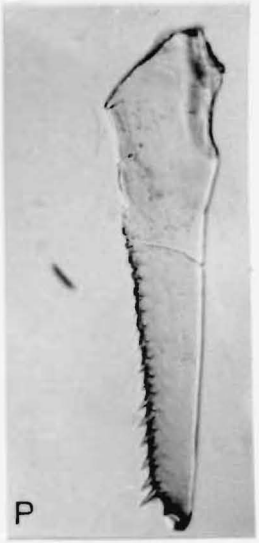
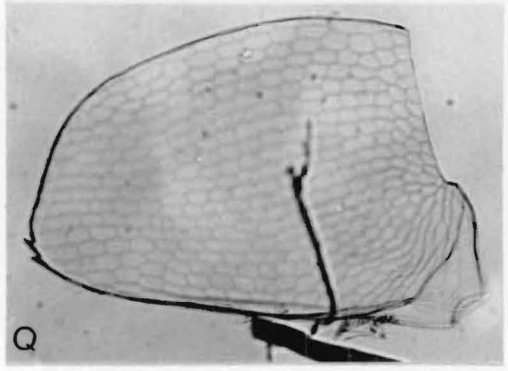


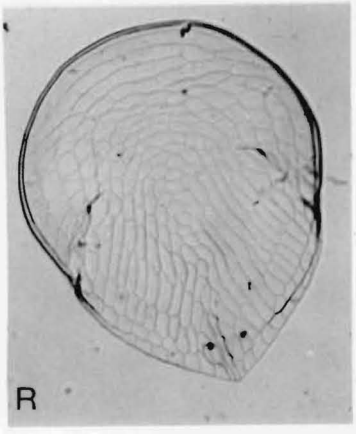
Fig. XI. **Lake Grasmere: Fossil Chydoridae**
Pleuroxus hastirostris
G: Carapace with postabdomen, x 140;
H: Headshield, x 140;
I: Carapace with postabdomen, x 420;
J: Postabdomen, x 420;
K: Carapace, x 100;
Alonella cf. *excisa*
L: Headshield, x 350;
M: Carapace, x 120.

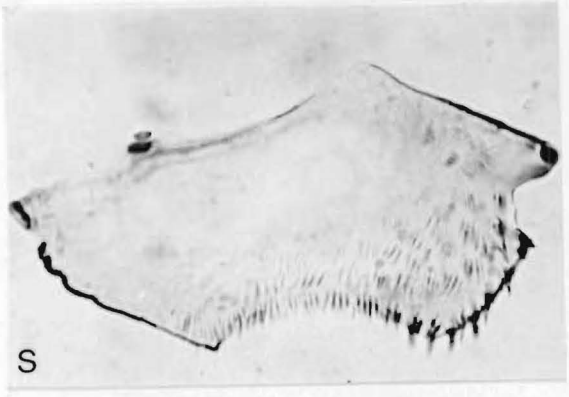


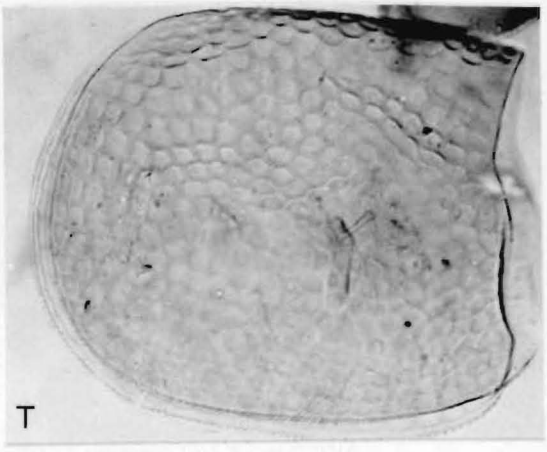












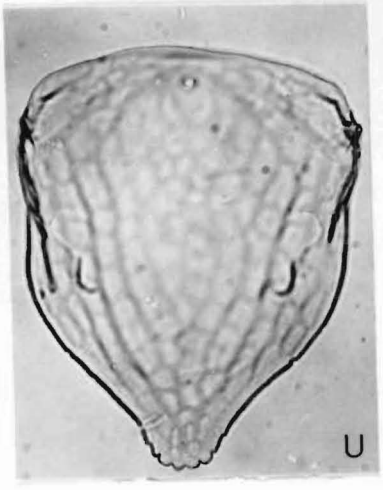


Fig. XII . **Lake Grasmere: Fossil Chydoridae**
Camptocerus australis
N: Headshield, x 210;
O: Carapace, x 100;
P: Postabdomen, x 180;
Graptoleberis testudinaria
Q: Carapace, x 160;
R: Headshield, x 170;
Monospilus dispar
S: Postabdomen, x 450;
T: Carapace, x 350;
U: Headshield, x 205.

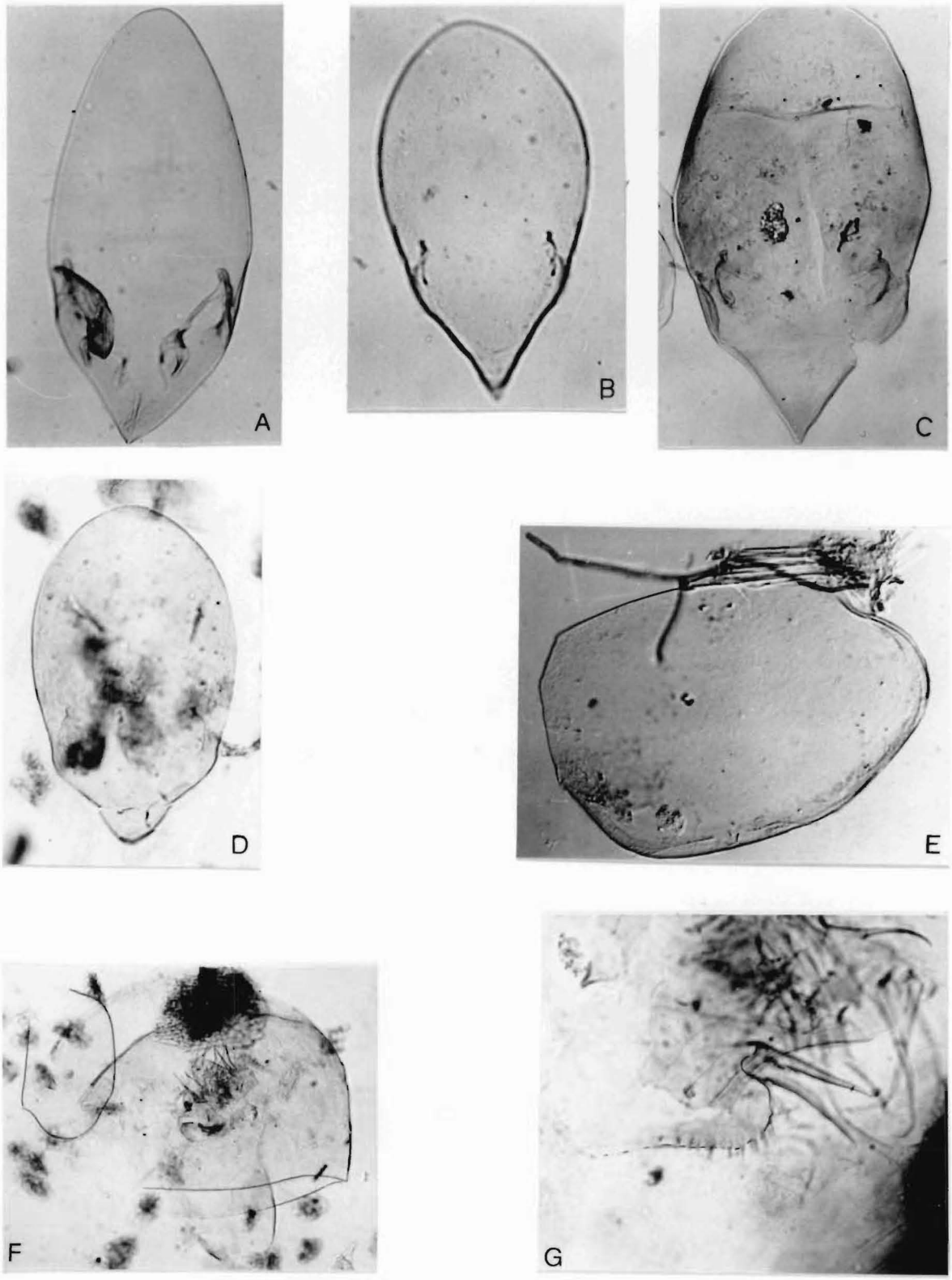
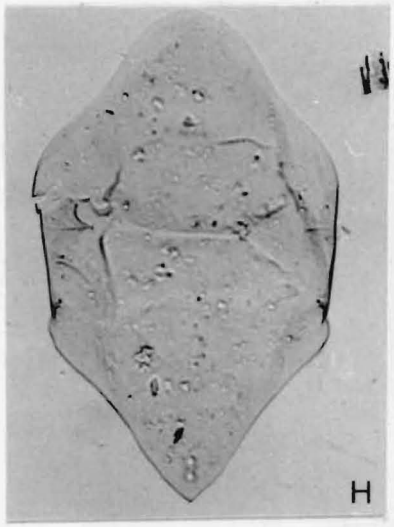
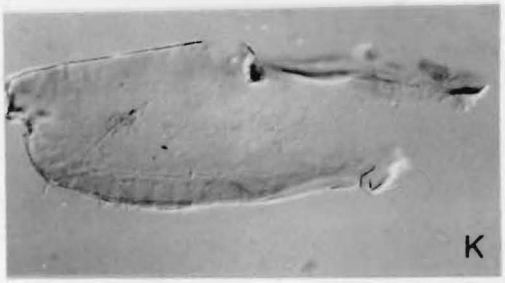
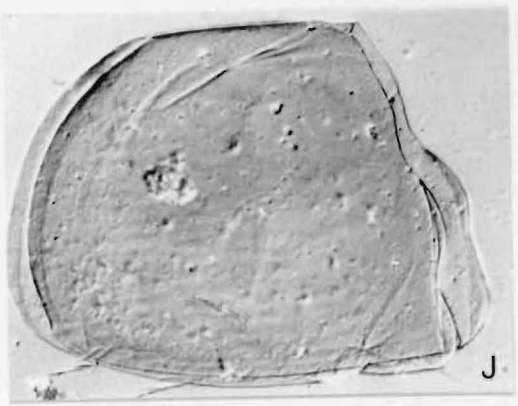
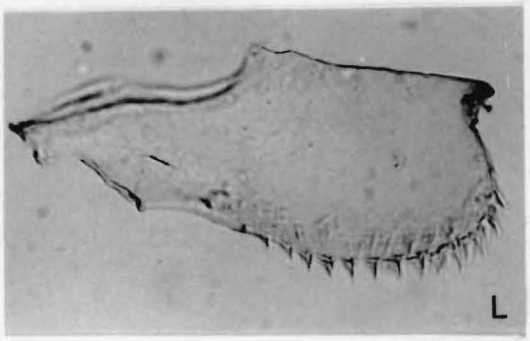


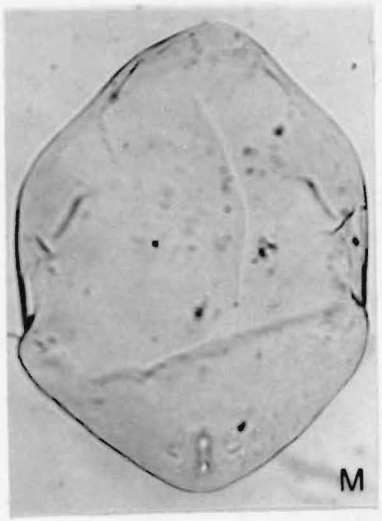
Fig.XIII. **Lake Grasmere: Fossil Chydoridae**
Chydorus sp.
A: Headshield, x 165;
B: Headshield, x 200;
C: Headshield, x 220;
D: Headshield, x 165;
E: Carapace, x 160;
F: Carapace with postabdomen, x 105;
G: Carapace with postabdomen, x 390.











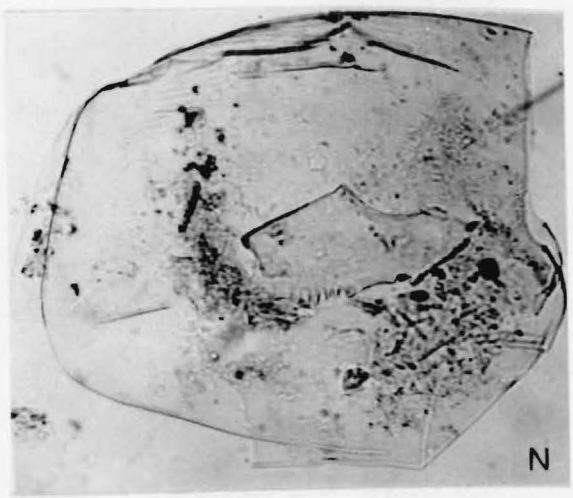
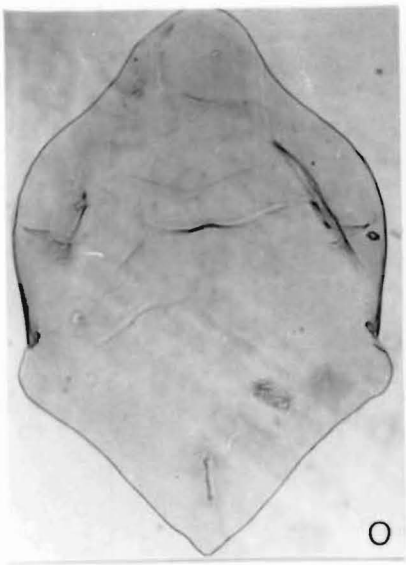
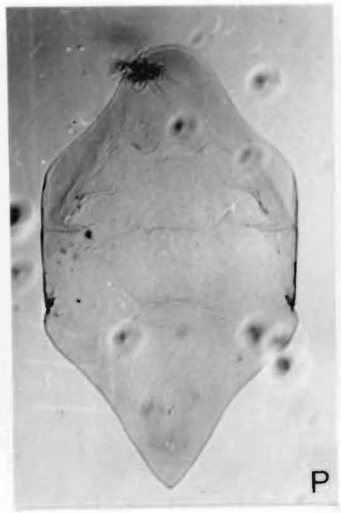
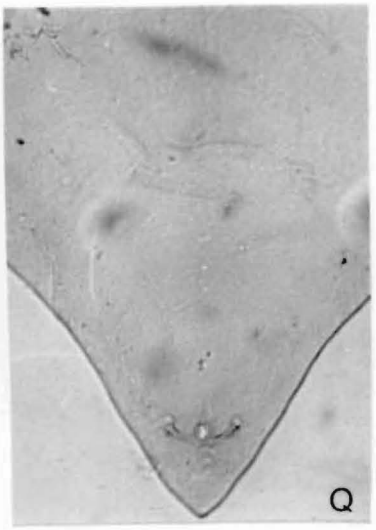
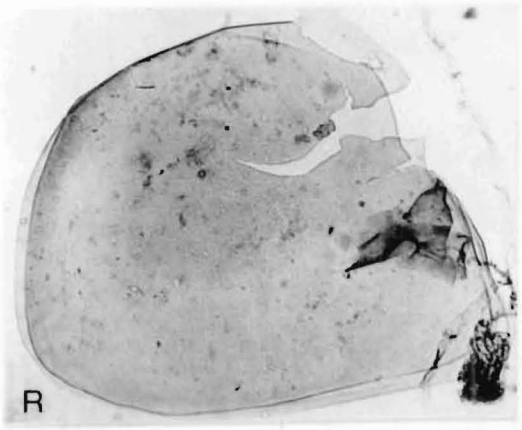


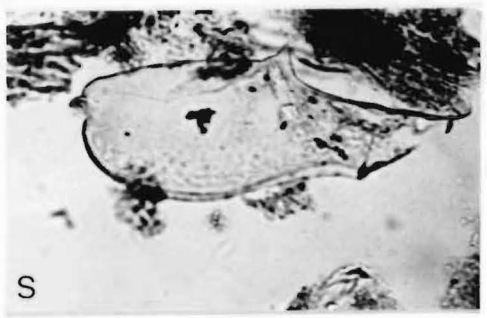
Fig. XIV. **Lake Grasmere: Fossil Chydoridae**
Biapertura affinis
H: Headshield, x 180;
I: Carapace, x 150;
J: Carapace, x 120;
K: Postabdomen, x 220;
L: Postabdomen, x 250.
Biapertura setigera
M: Headshield, x 340;
N: Carapace with postabdomen, x 230.











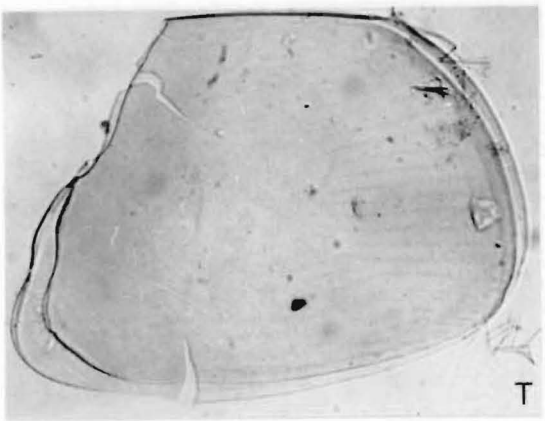
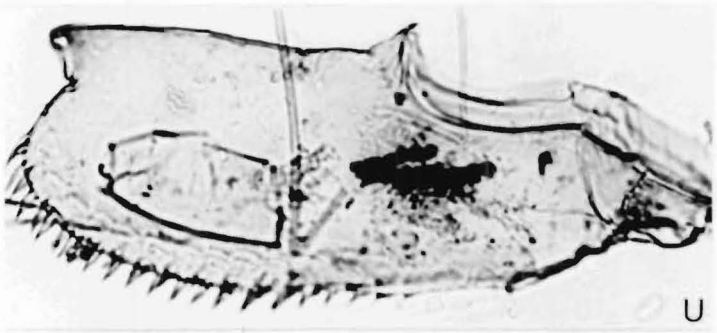
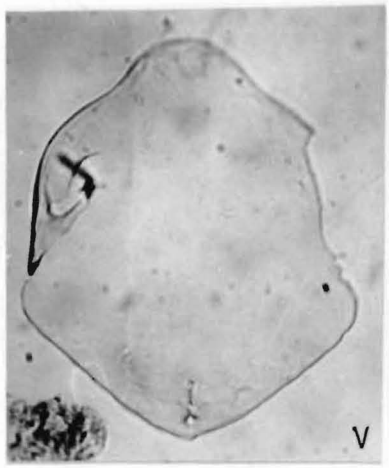
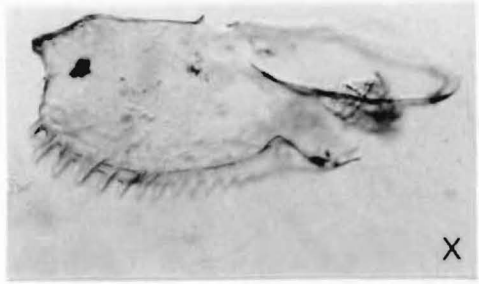
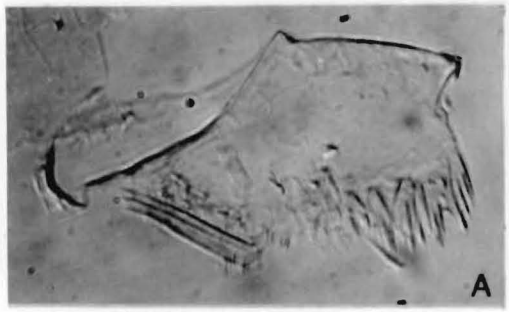


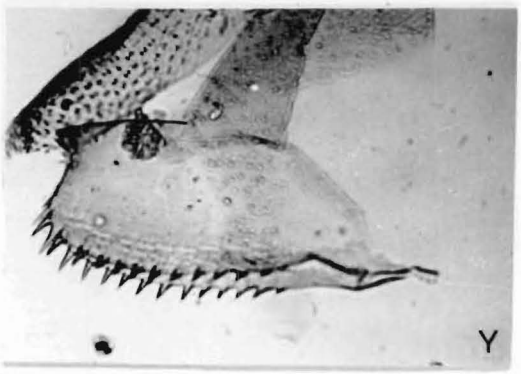
Fig. XV. **Lake Grasmere: Fossil Chydoridae**
Alona quadrangularis
O: Headshield, x 170;
P: Headshield, x 130;
Q: Headshield, x 250;
R: Carapace, x 110;
S: Postabdomen, x 230;
T: Carapace, x 160;
U: Postabdomen, x 315.

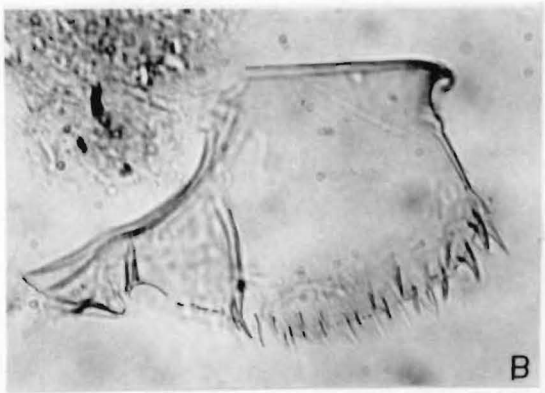












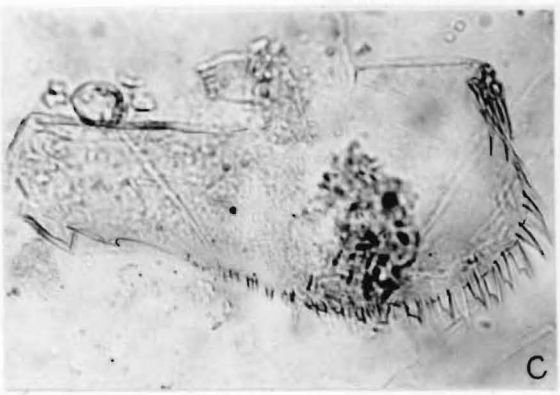


Fig. XVI. **Lake Grasmere: Fossil Chydoridae**
Alona rectangula
V: Headshield, x 430;
W: Carapace, x 270;
X: Postabdomen, x 250;
Y: Postabdomen, x 200;
Unidentified Remains
A: Postabdomen, x 430;
B: Postabdomen, x 520;
C: Postabdomen, x 330.

APPENDIX II

LAKE GRASMERE: Records of Sediment Analyses and Fossil Counts.

Table II.1. Lake Grasmere: Results of the Sediment Analyses (Water Content, and Loss-on-Ignition) on Samples from the Sediment Core.

Depth/cm	H_2O-Content % of Wet Weight	Loss-on-Ignition % of Dry Weight
1	61.9	6.6
10	58.4	6.3
14	42.8	6.4
17	46.8	6.8
20	64.9	9.5
22	74.6	13.9
25	76.7	17.2
27	75.8	15.4
30	63.5	9.8
33	41.9	6.0
40	35.2	5.7
50	42.6	7.1
55	49.0	6.9
60	65.5	9.9
70	54.9	7.1
80	58.5	7.8
90	62.2	9.1
100	63.0	9.4
110	50.4	6.9
120	50.8	8.0
130	57.9	8.2
140	50.7	6.9
145	52.6	8.4
150	65.0	9.1
155	51.8	9.2
160	53.2	8.2
170	48.0	7.6
180	42.9	5.6
190	32.1	6.7
195	31.7	6.6
200	28.6	5.0
204	33.5	5.8
210	34.5	4.6
220	42.2	5.4
230	35.2	5.8
235	40.2	5.0
240	34.6	4.8
250	44.9	6.5
260	33.7	5.5
270	36.2	5.1
280	44.4	6.2
285	44.7	6.4
290	40.5	6.2
295	52.0	15.7
300	54.4	14.4
305	53.5	11.6
310	47.3	10.1
313	49.8	9.2
317	42.2	6.6
319	26.6	4.5
322	23.2	3.7
326	21.0	2.5

Table II.2. Lake Grasmere: Total Number of Fossil Chironomidae Head Capsules, Number of the Chironomidae Subfamilies, and Number of Taxa in the Samples of the Sediment Core.

1: DEPTH/CM
2: Total Number of Chironomid Head capsules
3: ORTHOCLADIINAE
4: CHIRONOMINI
5: TANYTARSINI
6: TANYPODINAE
7: PODONOMINAE
8: HEPTAGYINI
9: Number of Taxa in the Sediment Samples

1	2	3	4	5	6	7	8	9
1	26	6	14	2	2	0	0	8
3	18	3	6	1	6	0	0	9
6	20	2	10	0	7	0	0	4
10	16	1	9	0	5	0	0	5
12	5	1	1	0	1	0	0	4
14	8	5	2	0	0	0	0	4
17	8	4	3	1	0	0	0	4
20	48	23	14	5	4	0	0	8
23	145	102	14	15	2	0	0	12
25	88	57	22	5	1	0	0	11
27	94	59	19	9	4	0	0	11
30	9	4	1	2	0	0	0	3
40	2	1	0	0	0	0	0	1
50	14	5	5	3	1	0	0	6
55	20	4	4	8	2	0	1	9
60	123	14	32	55	19	0	0	14
70	163	9	41	79	27	0	0	15
80	142	10	37	69	21	0	0	16
90	120	13	15	57	29	0	0	15
100	256	12	69	142	28	0	0	16
110	135	14	37	56	25	0	0	16
120	102	6	38	36	20	0	0	12
130	176	16	24	94	34	0	0	15
140	201	20	37	87	53	0	0	17
150	626	56	107	359	93	0	0	20
155	133	18	25	53	29	0	1	19
160	201	17	73	62	46	0	1	18
170	146	16	53	39	29	0	0	17
180	64	7	23	18	14	0	0	14
190	10	1	2	3	2	0	0	4
195	19	3	6	7	2	0	0	6
200	4	1	1	1	1	0	0	4
204	7	2	1	2	1	1	0	5
210	16	2	7	3	3	0	0	7
220	61	7	20	21	12	0	0	13
230	72	11	22	16	22	0	0	19
235	36	3	14	10	7	0	1	11
240	64	10	30	12	11	0	0	15
247	51	8	14	16	11	1	0	15
250	92	17	25	17	32	0	0	19
260	19	4	7	3	5	0	0	10
270	40	9	15	6	7	0	1	13
280	92	7	28	31	25	0	0	18
285	184	33	50	68	32	0	0	18
290	68	5	16	26	19	0	0	14
295	219	29	47	105	32	0	0	22
300	179	16	35	97	29	0	0	18
305	249	27	69	94	55	0	0	19
310	99	13	14	43	25	0	2	15
313	296	54	98	80	45	0	0	23
315	160	29	44	37	42	0	0	16
317	48	13	17	10	6	0	0	14
318	59	17	19	4	13	0	0	15
319	28	7	10	4	5	1	0	11
322	9	3	3	0	1	0	0	4
326	0	0	0	0	0	0	0	0

Table II.3. Lake Grasmere: Number of Head Capsules of Chironomidae Taxa in the Samples of the Sediment Core.

1: DEPTH/CM
2: CHIRONOMUS
3: PAUCISPINIGERA APPROXIMATA
4: POLYPEDILUM
5: CLADOPELMA
6: CHIRONOMINI sp.A
7: PARACHIRONOMUS
8: XENOCHIRONOMUS

24: APSECTROTANYPUS
25: TANYPODINAE sp. I
26: MACROPELOPIA
27: nr. PENTANEURA
28: GRESSITTIUS ANTARCTICUS
29: ABLABESMYIA

30: MAORIDIAMESA
31: nr. LIMAYA

9: CORYNOCERA
10: TANYTARSUS VESPERTINUS
11: PARATANYTARSUS
12: TANYTARSUS FUNEBRIS

13: ORTHOCLADIINAE sp. IX
14: CRICOTOPUS
15: CRICOTOPUS sp. 25
16: ORTHOCLADIINAE XIV
17: RHEOCRICOTOPUS
18: EUKIEFFERIELLA CLARIPENNIS
19: ORTHOCLADIINAE sp. XV
20: nr. SYNORTHOCLADIUS
21: ORTHOCLADIINAE V
22: ORTHOCLADIINAE I
23: MATAKIRI

32: PAROCHLUS

Only one head capsule was found of the following taxa:

RIETHIA	(250cm)
PAUCISPINIGERA sp.a	(322cm)
CRYPTOCHIRONOMUS	(180cm)
PODONOMUS	(204cm)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	10	0	0	3	1	0	0	0	0	1	1	1	5	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
3	4	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0
6	10	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0
10	9	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	2	0	1	0	0	0	0	0
12	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
14	2	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
17	3	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	13	0	0	0	1	0	0	0	1	4	0	18	4	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
23	11	1	0	0	0	2	0	0	5	8	2	95	4	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0
25	17	0	0	0	4	1	0	0	2	3	0	45	3	1	0	6	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
27	16	0	0	0	0	3	0	1	5	2	1	47	1	0	0	11	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0
30	1	0	0	0	0	0	0	0	0	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	4	0	0	0	1	0	0	0	2	1	0	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	2	0	0	1	1	0	0	2	0	6	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
60	20	0	3	2	7	0	0	46	2	7	0	4	8	0	0	0	0	2	0	0	0	0	13	4	0	1	1	0	0	0	0
70	24	0	6	5	4	0	1	69	2	8	0	2	5	0	0	0	2	0	0	0	0	0	12	10	0	0	1	0	0	0	0

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
80	12	0	7	11	7	0	0	61	1	7	0	2	3	1	1	1	2	0	0	0	0	0	14	4	0	0	1	0	0	0	0
90	11	0	0	1	3	0	0	52	1	2	2	8	4	1	0	0	0	0	0	0	0	0	16	1	2	1	1	0	0	0	0
100	49	0	7	9	3	0	1	121	6	15	0	2	6	0	0	0	3	0	0	1	0	0	12	4	0	4	4	0	0	0	0
110	22	0	4	9	2	0	0	49	0	5	2	4	3	1	0	3	1	0	0	0	0	2	12	9	0	3	0	0	0	0	0
120	23	0	1	4	8	2	0	32	0	4	0	3	2	0	0	0	0	0	0	0	0	0	9	7	0	2	0	0	0	0	0
130	13	0	9	1	1	0	0	83	3	7	1	5	11	0	0	0	0	0	0	0	0	0	17	2	1	2	1	0	0	0	0
140	23	0	5	6	3	0	0	71	3	12	1	4	13	0	1	0	1	1	0	0	0	0	30	12	0	1	5	0	0	0	0
150	48	0	14	42	2	0	1	322	17	18	2	9	34	3	3	0	1	3	0	0	0	0	62	9	4	9	5	0	0	0	0
155	9	0	4	9	2	0	1	42	1	10	0	3	8	3	1	0	0	1	0	0	2	0	12	5	1	2	0	0	0	1	0
160	45	0	6	17	3	0	2	47	3	10	2	3	7	0	1	0	1	3	0	0	0	0	30	9	0	2	1	0	0	0	0
170	29	0	9	11	3	1	0	28	8	3	0	4	9	1	0	0	0	2	0	0	0	0	17	5	2	1	2	0	0	0	0
180	12	0	3	3	4	1	0	13	2	3	0	1	6	0	0	0	0	0	0	0	0	0	8	1	0	2	0	0	0	0	1
190	2	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
195	6	0	0	0	0	0	0	6	1	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
200	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
204	0	0	1	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
210	4	0	0	2	0	0	1	2	0	1	0	2	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
220	9	1	8	0	2	0	0	20	0	1	0	0	3	0	0	0	3	1	0	0	0	0	5	1	0	1	4	0	0	0	0
230	10	4	2	3	2	0	0	9	4	3	0	2	2	2	2	0	0	1	0	1	0	0	15	2	2	1	2	0	0	0	0
235	0	12	0	1	1	0	0	7	1	2	0	0	2	0	0	0	0	1	0	0	0	0	4	1	0	0	0	0	1	0	0
240	18	8	2	2	0	0	0	6	4	1	1	3	1	0	0	0	1	5	0	0	0	0	6	2	0	0	1	0	0	0	0
247	5	0	3	5	1	0	0	12	2	2	0	1	4	0	0	0	1	1	0	0	0	0	7	3	0	1	0	0	0	0	1
250	6	12	4	0	2	0	0	8	3	6	0	8	4	0	0	0	0	1	0	1	0	1	15	4	1	2	2	1	0	0	0
260	1	6	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	1	0	0	5	0	0	0	0	0	0	0	0
270	3	9	2	1	0	0	0	4	1	1	0	3	3	0	0	0	0	0	0	1	1	0	7	0	0	0	0	0	1	0	0
280	9	12	2	1	4	0	0	20	7	4	0	1	2	1	0	0	0	1	1	1	0	0	10	5	0	4	1	0	0	0	0
285	25	8	6	2	9	0	0	48	8	9	3	11	12	0	0	2	1	6	0	0	0	0	13	11	2	3	0	0	0	0	0
290	6	3	3	1	3	0	0	14	5	7	0	3	2	0	0	0	0	0	0	0	0	0	6	3	1	0	1	0	0	0	0
295	19	2	11	9	5	0	1	71	20	10	4	8	10	2	1	2	0	4	0	2	0	0	19	6	2	3	1	0	0	0	0
300	16	0	5	11	3	0	0	75	11	9	2	4	8	0	0	1	0	2	0	0	0	0	17	4	2	3	1	1	0	0	0
305	48	0	12	8	1	0	0	71	9	13	1	2	15	4	1	2	0	0	0	1	2	0	31	3	2	7	5	0	0	0	0
310	5	1	8	0	0	0	0	25	7	10	1	1	7	4	0	0	0	0	0	0	1	0	16	0	1	1	0	0	0	2	0
313	50	2	17	23	4	2	0	47	14	16	3	15	12	5	3	3	3	11	0	1	0	0	19	9	4	7	3	0	0	0	0
315	20	6	11	7	0	0	0	26	6	5	0	8	15	0	3	0	0	2	0	1	0	0	10	7	10	1	0	0	0	0	0
317	5	7	4	1	0	0	0	6	2	2	0	4	1	3	5	0	0	0	0	0	0	0	2	0	2	2	0	0	0	0	0
318	6	5	3	3	1	0	0	2	1	1	0	14	0	0	0	1	0	2	0	0	0	0	0	3	3	2	2	0	0	0	0
319	7	0	2	1	0	0	0	3	0	1	0	5	0	0	0	0	1	0	1	0	0	0	4	0	1	0	0	0	0	0	1
322	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
326	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table II.4. Lake Grasmere: Numbers of Cladocera Remains in the Sediment Samples of the Core. Abbreviations used: N-Total Number/ml Sediment, NT-Number of Taxa in the Sample, HS-Headshields, CA-Carapaces, PA-Postabdomen, EP-Ephippia. The Underlined Remains were used for Graphical Displays and the Statistical Analyses.

Sample=1cm	N=6177		NT=11		Sample=10cm, N=1500, NT-9				Sample=12cm, N=485, NT=11			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	224	195	0	1	173	156	0	2	135	107	0	0
Simocephalus	0	0	0	1	0	0	0	0	0	0	0	1
A.quadrangularis	4	12	3	0	3	5	0	0	1	4	0	0
A.rectangula	2	3	0	0	0	0	0	0	0	0	0	0
B. affinis	7	11	6	0	6	8	3	0	4	5	1	0
B. setigera	2	8	0	0	0	2	0	0	1	2	0	0
Graptoleberis	5	8	0	0	1	6	0	0	2	3	0	0
Monospilus	1	3	1	0	0	0	0	0	1	0	0	0
Camptocercus	3	5	0	0	3	1	0	0	0	0	1	0
Alonella	0	0	0	0	0	0	0	0	0	0	0	0
Chydorus	21	62	1	0	7	15	0	0	11	16	0	0
Pleuroxus	0	0	0	0	1	0	0	0	1	0	0	0
Ilyocryptus	0	4	0	0	0	1	0	0	0	1	0	0

Sample=17cm	N=555		NT=9		Sample=20cm, N=7675, NT=10				Sample=25cm, N=4608, NT=9			
Bosmina	98	115	0	0	223	214	0	0	152	148	0	0
Daphnia	0	0	0	0	0	0	0	0	0	0	0	0
Simocephalus	0	0	0	0	0	0	0	0	0	0	0	0
A.quadrangularis	0	0	0	0	2	7	0	0	1	3	0	0
A.rectangula	1	2	1	0	3	6	0	0	0	0	0	0
B. affinis	2	3	0	0	4	10	6	0	4	7	3	0
B. setigera	0	0	0	0	5	28	1	0	6	11	2	0
Graptoleberis	1	3	0	0	2	11	0	0	6	14	0	0
Monospilus	1	1	0	0	0	0	0	0	1	0	0	0
Camptocercus	0	0	1	0	1	5	0	0	0	0	0	0
Alonella	0	0	0	0	0	0	0	0	1	0	0	0
Chydorus	12	34	0	0	16	40	0	0	21	53	0	0
Pleuroxus	5	8	0	0	13	15	1	0	39	74	7	0
Ilyocryptus	0	2	0	0	0	1	0	0	0	0	0	0

Sample=27cm	N=2325		NT=11		Sample=40cm, N=93, NT=9				Sample=50cm, N=800, NT=13			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	117	127	0	0	13	13	0	0	52	38	0	4
Daphnia	0	0	0	0	0	0	0	0	0	0	0	0
Simocephalus	0	0	0	0	0	0	0	0	0	0	0	7
A.quadrangularis	3	6	0	0	1	2	0	0	6	10	3	0
A.rectangula	1	3	0	0	0	0	0	0	2	2	0	0
B. affinis	10	10	6	0	2	4	1	0	10	10	2	0
B. setigera	2	8	0	0	1	5	0	0	0	6	0	0
Graptoleberis	10	9	0	0	6	11	0	0	16	23	0	0
Monospilus	0	0	1	0	0	1	0	0	3	4	2	0
Camptocercus	1	2	1	0	0	0	0	0	0	0	0	0
Alonella	1	2	0	0	0	1	0	0	2	4	0	0
Chydorus	28	40	1	0	9	13	0	0	10	8	0	0
Pleuroxus	37	41	4	0	3	7	0	0	2	5	2	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	1	0	0

Sample=60cm	N=1425		NT=10		Sample=70cm, N=3463, NT=10				Sample=80cm, N=3019, NT=12			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	58	90	0	0	247	228	0	0	213	187	0	0
Daphnia	0	0	0	7	0	0	0	0	0	0	0	2
Simocephalus	0	0	0	0	0	0	0	6	0	0	0	2
A.quadrangularis	5	18	4	0	11	15	3	0	10	7	2	0
A.rectangula	1	0	1	0	0	1	1	0	1	0	1	0
B. affinis	16	28	25	0	10	8	8	0	13	7	17	0
B. setigera	1	13	1	0	0	5	0	0	1	7	0	0
Graptoleberis	1	4	0	0	1	2	0	0	4	3	0	0
Monospilus	1	0	0	0	0	1	0	0	1	1	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	1	5	0	0	2	0	0	0	1	1	0	0
Chydorus	2	3	0	0	0	0	0	0	0	1	0	0
Pleuroxus	0	0	0	0	0	0	0	0	0	0	1	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=100cm	N=1875		NT=9		Sample=110cm,	N=2145,	NT=8		Sample=120cm,	N=3129,	NT=10	
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	119	160	0	0	164	173	0	0	234	231	0	0
Daphnia	0	0	0	3	0	0	0	2	0	0	0	2
Simocephalus	0	0	0	0	0	0	0	0	0	0	0	10
A.quadrangularis	19	23	2	0	19	10	0	0	13	20	3	0
A.rectangula	3	8	0	0	5	5	4	0	4	2	1	0
B. affinis	9	5	9	0	11	7	16	0	18	10	22	0
B. setigera	0	6	0	0	2	8	0	0	0	2	1	0
Graptoleberis	0	3	0	0	0	0	0	0	2	3	0	0
Monospilus	2	1	0	0	0	0	0	0	1	1	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	0	0	0	0	2	0	0	0	0	0	0
Chydorus	0	3	0	0	0	1	0	0	1	3	0	0
Pleuroxus	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=140,	N=2111		NT=10		Sample=150cm,	N=3075,	NT=10		Sample=160cm,	N=641,	NT=10	
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	212	170	0	6	133	123	0	5	70	79	0	0
Daphnia	0	0	0	4	0	0	0	10	0	0	0	14
Simocephalus	0	0	0	0	0	0	0	5	0	0	0	0
A.quadrangularis	26	35	8	0	35	43	3	0	24	30	3	0
A.rectangula	8	6	8	0	1	14	3	0	9	8	4	0
B. affinis	24	16	18	0	29	26	25	0	16	23	19	0
B. setigera	0	13	0	0	1	19	3	0	2	12	0	0
Graptoleberis	1	3	0	0	2	2	0	0	0	1	0	0
Monospilus	1	1	0	0	0	0	0	0	1	1	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	2	0	0	0	4	0	0	0	1	0	0
Chydorus	1	0	0	0	0	1	0	0	1	0	0	0
Pleuroxus	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=170cm	N=716		NT=10		Sample=180cm, N=465, NT=9				Sample=195cm, N=34, NT=6			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	98	78	0	0	89	82	0	0	6	8	0	0
Daphnia	0	0	0	5	0	0	0	5	0	0	0	3
Simocephalus	0	0	0	0	0	0	0	0	0	0	0	0
A.quadrangularis	8	10	2	0	5	8	1	0	3	5	0	0
A.rectangula	3	9	0	0	5	3	3	0	0	0	0	0
B. affinis	20	14	21	0	25	25	16	0	3	0	0	0
B. setigera	3	6	0	0	0	5	0	0	0	0	0	0
Graptoleberis	2	3	0	0	2	1	0	0	0	0	0	0
Monospilus	1	0	0	0	0	0	0	0	0	0	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	1	0	0	0	1	0	0	1	2	1	0
Chydorus	15	10	0	0	0	1	0	0	2	0	0	0
Pleuroxus	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=200cm	N=8		NT=6		Sample=204cm, N=64, NT=7				Sample=220cm, N=630, NT=7			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	1	1	0	0	17	11	0	0	120	91	0	0
Daphnia	0	0	0	0	0	0	0	5	0	0	0	1
Simocephalus	0	0	0	1	0	0	0	0	0	0	0	0
A.quadrangularis	0	2	0	0	4	2	0	0	10	13	0	0
A.rectangula	0	0	0	0	0	0	0	0	1	1	0	0
B. affinis	0	1	0	0	1	7	0	0	4	4	5	0
B. setigera	0	0	0	0	1	2	0	0	0	5	0	0
Graptoleberis	1	0	0	0	0	1	0	0	0	0	0	0
Monospilus	0	0	0	0	0	0	0	0	1	2	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	0	0	0	0	0	0	0	0	0	0	0
Chydorus	1	0	0	0	0	1	0	0	0	0	0	0
Pleuroxus	0	0	0	0	0	0	0	0	0	0	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=230cm	N=285		NT=7		Sample=240cm, N=152, NT=9				Sample=247cm, N=251, NT=9			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	40	36	0	4	11	24	0	0	18	19	0	0
Daphnia	0	0	0	11	0	0	0	4	0	0	0	17
Simocephalus	0	0	0	0	0	0	0	0	0	0	0	0
A.quadrangularis	18	13	0	0	21	27	0	0	17	29	0	0
A.rectangula	1	1	1	0	1	2	0	0	2	3	0	0
B. affinis	16	19	10	0	13	19	12	0	10	38	12	0
B. setigera	4	16	0	0	2	4	1	0	0	2	1	0
Graptoleberis	6	3	0	0	3	5	0	0	1	2	0	0
Monospilus	0	0	0	0	2	0	0	0	2	2	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	0	0	0	0	0	0	0	0	0	0	0
Chydorus	0	0	0	0	1	1	0	0	0	0	0	0
Pleuroxus	0	0	0	0	0	0	0	0	4	3	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=250cm	N=405		NT=9		Sample=270cm, N=128, NT=10				Sample=280cm, N=559, NT=10			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	70	94	0	0	20	19	0	0	57	75	0	0
Daphnia	0	0	0	4	0	0	0	2	0	0	0	3
Simocephalus	0	0	0	3	0	0	0	1	0	0	0	0
A.quadrangularis	8	10	0	0	6	5	0	0	4	6	1	0
A.rectangula	1	2	2	0	0	0	0	0	2	0	1	0
B. affinis	27	19	6	0	23	21	8	0	13	15	15	0
B. setigera	1	8	0	0	1	5	0	0	2	6	1	0
Graptoleberis	1	3	0	0	6	3	0	0	8	17	0	0
Monospilus	1	0	0	0	2	3	0	0	0	0	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	0	0	0	0	0	0	0	1	0	0	0
Chydorus	0	0	0	0	0	3	0	0	0	3	0	0
Pleuroxus	0	0	0	0	0	0	0	0	0	1	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=285cm	N=645		NT=8		Sample=295cm, N=731, NT=12				Sample=300cm, N=533, NT=11			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	62	79	0	0	4	3	0	0	3	5	0	0
Daphnia	0	0	0	6	0	0	0	15	0	0	0	26
Simocephalus	0	0	0	0	0	0	0	1	0	0	0	2
A.quadrangularis	19	11	3	0	58	43	7	0	36	33	6	0
A.rectangula	1	4	5	0	5	13	1	0	0	17	0	0
B. affinis	13	12	20	0	16	13	39	0	17	18	30	0
B. setigera	3	9	0	0	4	10	0	0	5	15	0	0
Graptoleberis	5	9	0	0	1	3	0	0	5	3	0	0
Monospilus	0	0	0	0	0	4	0	0	1	0	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	0	0	0	1	2	0	0	0	0	0	0
Chydorus	2	4	0	0	1	0	0	0	0	1	0	0
Pleuroxus	0	0	0	0	1	0	0	0	1	1	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=305cm	N=795		NT=10		Sample=313cm, N=319, NT=11				Sample=318cm, N=642, NT=11			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	1	1	0	0	30	34	0	0	208	348	0	0
Daphnia	0	0	0	29	0	0	0	13	0	0	0	0
Simocephalus	0	0	0	2	0	0	0	5	0	0	0	1
A.quadrangularis	41	60	14	0	24	18	7	0	9	6	0	0
A.rectangula	2	14	0	0	0	5	0	0	4	8	0	0
B. affinis	9	16	21	0	12	16	26	0	8	7	14	0
B. setigera	1	10	4	0	3	10	4	0	1	9	0	0
Graptoleberis	0	1	0	0	3	1	0	0	3	8	0	0
Monospilus	0	0	0	0	1	0	0	0	2	0	0	0
Camptocercus	0	0	0	0	0	0	0	0	0	0	0	0
Alonella	0	1	0	0	0	1	0	0	0	1	0	0
Chydorus	0	4	0	0	3	9	0	0	0	0	0	0
Pleuroxus	0	0	0	0	0	0	0	0	1	2	0	0
Ilyocryptus	0	0	0	0	0	0	0	0	0	0	0	0

Sample=319cm	N=60		NT=10		Sample=322cm, N=23, NT=5			
Taxon/Remains	HS	CA	PA	EP	HS	CA	PA	EP
Bosmina	9	5	0	0	2	2	0	0
Daphnia	0	0	0	1	0	0	0	0
Simocephalus	0	0	0	4	0	0	0	1
A. quadrangularis	3	1	0	0	0	0	0	0
A. rectangula	0	0	0	0	0	0	0	0
B. affinis	3	14	10	0	2	4	6	0
B. setigera	1	3	0	0	1	1	1	0
Graptoleberis	0	2	0	0	0	0	0	0
Monospilus	0	0	1	0	1	1	1	0
Camptocercus	0	0	0	0	0	0	0	0
Alonella	0	1	0	0	0	0	0	0
Chydorus	0	2	0	0	0	0	0	0
Pleuroxus	0	0	0	0	0	0	0	0
Ilyocryptus	0	0	0	0	0	0	0	0

APPENDIX III

SOUTH ISLAND LAKES: Records of Fossil Counts from Surficial Sediment Samples.

Table III.1. South Island Lakes: Total Number of Fossil Chironomidae Head Capsules, Number of the Chironomidae Subfamilies, and Number of Taxa in the Surficial Sediment Samples.

1: Total Number of Chironomid Head Capsules
2: CHIRONOMINI
3: TANYTARSINI
4: ORTHOCLADIINAE
5: TANYPODINAE
6: PODONOMINAE
7: DIAMESINAE
8: Number of Taxa in the Sediment Samples

Lakes	1	2	3	4	5	6	7	8
L. Grasmere	60	29	1	12	18	0	0	13
L. Hawdon	76	14	32	17	13	0	0	11
L. Sarah	50	14	5	26	5	0	0	12
L. Marymere	69	4	2	58	5	0	0	10
L. Pearson	69	35	5	16	13	0	0	10
L. Lyndon	61	33	4	9	15	0	0	13
L. Letitia	86	36	22	18	9	1	0	11
Horseshoe L.	68	22	11	34	1	0	0	11
L. Taylor	76	30	0	24	19	0	3	13
L. Sheppard	60	27	19	11	2	0	1	14
L. Katrine	61	9	0	5	47	0	0	10
L. Mason	59	12	5	21	21	0	0	15
L. Rotoiti	57	34	14	3	6	0	0	14
L. Rotorua	54	36	11	7	0	0	0	9
L. Heron	52	28	2	20	2	0	0	6
L. Camp	67	32	8	20	7	0	0	12
L. Emma	55	22	13	14	6	0	0	11
L. Clearwater	80	14	25	31	10	0	0	14
L. Coleridge I	72	34	2	31	5	0	0	10
L. Coleridge II	74	25	1	34	3	6	5	13
L. Georgina	63	14	10	34	5	0	0	12
L. Selfe	57	24	5	11	16	1	0	12
L. Evelyn	61	2	5	41	13	0	0	12
L. Catherine	50	3	8	25	13	0	1	14
L. Ida	67	32	4	18	13	0	0	9
L. Haupiri	86	23	8	33	16	4	2	23
L. Poerua	71	6	2	56	7	0	0	10
Lady Lake	52	16	0	29	2	1	4	15
L. Brunner I	48	7	3	35	2	1	0	15
L. Brunner II	49	11	0	36	0	0	2	14
L. Matheson	82	47	4	15	16	0	0	16
L. Alexandrina	58	40	7	10	1	0	0	10
L. Tekapo I	65	22	2	33	8	0	0	11
L. Tekapo II	53	19	2	24	8	0	0	10
L. Ohau	51	13	0	23	14	0	0	8

Table III.2. South Island Lakes: Head Capsules of Chironomidae Taxa in the Surficial Sediment Samples

1: CHIRONOMUS
2: PAUCISPINIGERA sp. a
3: POLYPEDILUM
4: RIETHIA
5: CLADOPELMA
6: CHIRONOMINI sp.A
7: PARACHIRONOMUS
8: CRYPTOCHIRONOMUS
9: XENOCHIRONOMUS
10: KIEFFERULUS

28: APSECTROTANYPUS
29: TANYPODINAE sp. I
30: MACROPELOPIA
31: nr. PENTANEURA
32: GRESSITTIUS ANTARCTICUS
33: TANYPODINAE sp. II

11: CORYNOCERA
12: TANYTARSUS VESPERTINUS
13: TANYTARSUS FUNEBRIS
14: PARATANYTARSUS

15: ORTHOCLADIINAE sp. IX
16: CRICOTOPUS
17: CRICOTOPUS AUCKLANDENSIS
18: CORYNONEURA
19: ORTHOCLADIINAE XIV
20: ORTHOCLADIINAE VIII
21: EUKIEFFERIELLA
22: EUKIEFFERIELLA CLARIPENNIS
23: ORTHOCLADIINAE sp. XV
24: MATAKIRI
25: ORTHOCLADIINAE V
26: nr. SYNORTHOCLADIUS
27: ORTHOCLADIINAE XIII

34: MAORIDIAMESA
35: HEPTAGYINI spp.

36: PAROCHLUS
37: PODONOMUS

Lakes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
L. Grasmere	21	0	1	0	2	4	1	0	0	0	0	0	0	1	3	8	0	0	0	1	1	0	0	0	0	0	0	15	1	1	0	1	0	0	0	0	0
L. Hawdon	5	0	9	0	0	0	0	0	0	0	0	19	12	1	9	0	0	0	0	0	0	0	8	0	0	0	0	4	0	2	3	4	0	0	0	0	0
L. Sarah	7	0	0	0	2	5	0	0	0	0	2	2	1	0	12	11	0	1	0	0	0	0	2	0	0	0	0	2	0	0	0	3	0	0	0	0	0
L. Marymere	3	0	0	0	0	1	0	0	0	0	0	1	1	0	56	1	0	0	0	1	0	0	0	0	0	0	0	2	0	2	1	0	0	0	0	0	0
L. Pearson	27	0	0	0	6	1	1	0	0	0	0	5	0	0	13	3	0	0	0	0	0	0	0	0	0	0	0	9	3	0	1	0	0	0	0	0	0
L. Lyndon	29	1	0	0	1	2	0	0	0	0	0	0	2	2	5	3	0	0	0	0	0	0	1	0	0	0	0	9	2	2	0	2	0	0	0	0	0
L. Letitia	19	0	1	0	10	6	0	0	0	0	22	0	0	0	13	5	0	0	0	0	0	0	0	0	0	0	0	2	6	0	1	0	0	0	0	1	0
L. Taylor	25	0	0	0	1	3	1	0	0	0	0	0	0	0	5	7	0	0	0	3	6	1	2	0	0	0	0	17	2	0	0	0	0	3	0	0	0
L. Sheppard	23	0	0	0	2	0	1	0	1	0	4	7	2	6	6	0	1	0	0	0	4	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0

Lakes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
L. Katrine	8	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	2	0	0	0	36	0	3	1	7	0	0	0	0	0
L. Mason	9	1	0	0	1	1	0	0	0	0	0	2	1	2	7	6	0	0	0	0	6	0	2	0	0	0	0	16	0	1	3	1	0	0	0	0	0
Horseshoe L.	16	0	0	0	2	3	1	0	0	0	2	4	4	0	7	6	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
L. Rotoiti	6	0	1	0	23	1	0	0	0	3	0	3	6	5	1	1	1	0	0	0	0	0	0	0	0	0	0	1	4	0	0	1	0	0	0	0	0
L. Rotorua	20	0	2	0	0	6	1	0	0	7	0	0	10	1	0	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. Heron	25	0	0	0	0	3	0	0	0	0	2	0	0	0	13	7	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
L. Camp	22	0	7	0	3	0	0	0	0	0	1	2	4	1	10	6	4	0	0	0	0	0	0	0	0	0	0	5	0	0	2	0	0	0	0	0	0
L. Emma	17	0	2	0	0	3	0	0	0	0	4	0	5	4	7	5	0	0	0	0	0	0	2	0	0	0	0	5	1	0	0	0	0	0	0	0	0
Clearwater	10	0	3	0	1	0	0	0	0	0	7	15	2	1	29	1	0	0	0	0	0	0	1	0	0	0	0	0	1	2	5	2	0	0	0	0	0
Coleridge I	30	0	0	0	0	4	0	0	0	0	0	0	0	2	29	1	0	0	0	0	0	0	0	0	1	0	0	1	1	2	1	0	0	0	0	0	0
Coleridge II	23	0	0	0	0	2	0	0	0	0	0	0	0	1	16	1	0	0	1	9	0	7	0	0	0	0	0	1	0	1	1	0	0	5	0	6	0
L. Georgina	12	0	0	0	0	1	1	0	0	0	1	6	2	1	29	4	0	0	0	0	0	0	1	0	0	0	0	2	0	0	1	2	0	0	0	0	0
L. Selfe	18	0	0	0	2	2	2	0	0	0	0	1	4	0	4	6	1	0	0	0	0	0	0	0	0	0	0	9	0	4	3	0	0	0	0	1	0
L. Evelyn	2	0	0	0	0	0	0	0	0	0	1	3	0	1	31	8	2	0	0	0	0	0	0	0	0	0	0	5	3	1	2	2	0	0	0	0	0
L. Catherine	1	1	0	0	0	1	0	0	0	0	1	3	4	0	5	14	1	0	0	1	0	1	3	0	0	0	0	6	0	0	7	0	0	1	0	0	0
L. Ida	27	0	3	0	0	1	1	0	0	0	4	0	0	0	8	10	0	0	0	0	0	0	0	0	0	0	0	9	0	0	4	0	0	0	0	0	0
Alexandrina	28	0	0	0	2	10	0	0	0	0	5	2	0	0	4	4	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
L. Tekapo I	10	7	0	0	0	5	0	0	0	0	0	1	1	0	19	14	0	0	0	0	0	0	0	0	0	0	0	3	1	1	3	0	0	0	0	0	0
L. Tekapo II	3	15	0	0	0	1	0	0	0	0	0	0	2	0	15	8	1	0	0	0	0	0	0	0	0	0	0	3	2	0	3	0	0	0	0	0	0
L. Ohau	8	0	0	0	0	5	0	0	0	0	0	0	0	0	14	2	0	0	0	0	5	0	0	0	0	0	3	10	0	0	4	0	0	0	0	0	0

Lakes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
L. Haupiri	7	7	2	0	1	4	0	1	1	0	0	1	3	4	9	15	2	0	1	3	1	1	1	0	0	0	0	7	4	0	5	0	0	2	0	4	0
L. Poerua	5	0	0	0	0	0	0	0	1	0	0	0	1	1	32	21	3	0	0	0	0	0	0	0	0	0	0	4	1	0	2	0	0	0	0	0	0
Lady Lake	9	3	0	1	0	2	1	0	0	0	0	0	0	0	5	4	4	0	1	0	12	2	0	1	0	0	0	0	0	0	2	0	0	0	4	0	1
L. Brunner I	0	3	3	0	0	1	0	0	0	0	0	0	1	2	14	11	4	0	1	0	2	0	0	1	0	2	0	0	1	0	1	0	0	0	0	0	1
Brunner II	2	4	0	0	0	2	0	1	2	0	0	0	0	0	12	3	2	2	0	1	10	4	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0
L. Matheson	2	37	0	1	1	3	3	0	0	0	0	1	2	1	9	1	0	2	0	0	0	1	0	0	0	2	0	5	0	0	0	0	11	0	0	0	0

APPENDIX IV

BLUE LAKE, MT. KOSCIUSKO, AUSTRALIA:
Records of Sediment Analyses and Fossil Counts in Samples from the Sediment Core. Fig. 3.5. Depth Profiles of Selected Sediment Fractions, Blue Lake Cores 1 & 3 , from Raine (1974).

Table IV.1. Blue Lake: Results of the Sediment Analyses (Water Content, and Loss-on-Ignition) on Samples from the Sediment Core.

Depth/cm	H_2O-Content % of Wet Weight	Loss-on-Ignition % of Dry Weight
1	78.9	27.1
10	83.5	29.3
20	82.1	28.4
40	80.7	25.8
60	80.7	27.8
80	82.1	29.3
100	78.3	26.4
120	82.4	31.9
140	81.5	29.6
160	81.9	31.4
180	80.9	31.8
200	79.8	30.6
221	81.0	33.2
223	79.3	32.0
243	76.5	30.9
263	76.0	29.8
283	75.4	29.4
303	70.4	23.5
323	66.1	23.4
338	72.7	24.0
363	67.6	13.5
383	55.1	8.9
403	34.7	5.8
408	44.3	6.2
438	17.9	3.0
441	16.5	2.9

Table IV.2. Blue Lake: Total Number of Fossil Chironomidae Head Capsules, Number of the Chironomidae Subfamilies, and Number of Taxa in the Samples of the Sediment Core.

1: DEPTH/CM
2: Total Number of Chironomidae Head Capsules
3: ORTHOCLADIINAE
4: PODONOMINAE
5: CHIRONOMINI
6: TANYTARSINI
7: TANYPODINAE
8: Number of Taxa in the Sediment Samples

1	2	3	4	5	6	7	8
437	0	0	0	0	0	0	0
417	0	0	0	0	0	0	0
412	0	0	0	0	0	0	0
407	13	6	3	2	0	0	5
406	12	5	3	3	0	0	6
404	28	14	8	4	2	0	8
402	6	2	1	3	0	0	4
392	32	6	9	15	1	1	9
382	40	12	10	12	0	1	10
372	47	24	8	11	1	2	13
362	79	32	6	30	3	3	12
352	188	94	17	38	16	5	22
342	73	44	7	13	1	4	15
337	77	47	7	16	2	1	16
332	85	48	5	20	3	5	16
322	123	73	11	23	7	0	17
312	126	67	18	27	5	2	19
302	126	67	10	24	8	5	19
282	59	28	10	8	2	2	16
262	84	47	7	17	3	5	19
242	37	20	2	7	2	1	13
223	61	28	5	20	1	0	12
221	148	58	19	51	4	2	19
210	64	26	9	18	2	3	14
200	67	26	6	21	3	4	17
190	59	23	5	18	2	4	15
180	66	26	14	16	2	0	12
160	73	35	14	17	0	1	16
140	51	24	4	20	1	1	17
120	75	22	12	30	1	1	14
100	75	26	11	28	0	1	12
80	66	30	9	20	0	2	17
70	39	13	3	15	0	3	14
60	73	27	4	30	2	1	19
40	44	11	5	25	0	1	10
30	52	14	2	29	0	0	9
20	61	15	5	31	0	0	11
10	52	10	3	28	0	0	10
1	38	12	1	16	0	0	8

Table IV.3. Blue Lake: Numbers of Head Capsules of Chironomidae Taxa in the Samples of the Sediment Core.

Sample Code 1-407cm, 2-406cm, 3-404cm, 4-402cm, 5-392cm, 6-382cm, 7-372cm, 8-362cm, 9-352cm, 10-342cm, 11-337cm, 12-332cm, 13-322cm, 14-312cm, 15-302cm, 16-282cm, 17-262cm, 18-242cm, 19-223cm, 20-221cm, 21-210cm, 22-200cm, 23-190cm, 24-180cm, 25-160cm, 26-140cm, 27-120cm, 28-100cm, 29-80cm, 30-70cm, 31-60cm, 32-40cm, 33-30cm, 34-20cm, 35-10cm, 36-1cm in the sediment core.

Taxon/Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Chironomus	1	3	4	3	12	7	9	17	20	8	8	12	7	13	14	5	9	5	18	39	14	17	14	13	11	11	21	18	14	11	22	17	17	25	21	12
Chironomini A	0	0	0	0	3	4	2	7	13	5	5	7	11	7	6	2	2	0	1	3	0	1	1	0	5	3	4	9	3	2	5	5	11	1	4	3
Polypedilum	0	0	0	0	0	0	0	6	4	0	1	1	3	4	1	0	4	2	1	4	2	1	2	1	1	1	3	1	2	1	1	3	0	4	1	0
Riethia	1	0	0	0	0	1	0	0	1	0	2	0	2	3	3	1	2	0	0	5	2	2	1	2	0	5	2	0	1	1	2	0	1	1	2	1
Xenochironomus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1	0	0	1	0	0
Tanytarsus	0	0	0	0	0	0	1	3	13	1	1	1	4	2	6	1	3	0	0	3	2	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0
Tanytarsini I	0	0	2	0	1	0	0	0	3	0	1	2	3	3	2	0	0	2	0	1	0	3	0	2	0	1	0	0	0	0	1	0	0	0	0	0
Podonomus	3	3	8	1	8	10	8	4	7	4	4	3	7	2	4	6	3	1	1	7	4	4	3	8	7	1	6	4	5	2	2	4	2	0	1	1
Parochlus	0	0	0	0	1	0	0	2	9	3	3	2	4	15	6	4	4	1	4	8	3	1	2	2	7	3	5	7	4	1	1	1	0	5	2	0
Eukiefferiella	0	1	1	0	4	3	9	4	54	27	12	20	36	28	25	13	20	8	11	28	12	12	11	12	15	6	9	16	16	6	8	5	3	8	7	5
Ortho I	0	1	0	1	0	2	4	9	3	4	8	6	7	6	9	2	8	2	2	4	0	0	0	0	2	1	2	0	2	0	1	0	0	0	1	0
E. claripennis	1	0	0	0	0	2	1	4	5	1	8	4	8	8	6	6	2	2	5	3	2	3	3	4	2	7	0	0	3	2	4	1	2	0	0	0
Ortho III	0	2	0	0	1	0	2	0	3	0	5	3	6	1	9	0	1	2	0	0	2	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0
Cricotopus 4	0	1	5	0	0	0	1	0	2	0	0	0	1	2	2	0	2	0	0	1	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0
Cricotopus 12	5	0	3	0	0	1	3	14	13	5	12	3	9	7	9	1	8	3	5	9	1	0	2	2	2	1	3	2	1	2	4	0	4	2	0	2
C.annuliventr.	0	0	0	0	0	0	0	0	1	1	1	0	3	0	0	1	1	0	2	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Taxon/Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Corynoneura	0	0	4	0	0	3	0	0	0	2	1	1	2	4	3	2	0	2	0	5	3	3	2	0	4	1	2	3	2	1	1	1	1	2	1	0
Paralimnophyes	0	0	1	1	1	0	1	0	4	1	0	7	0	6	0	1	2	1	0	3	0	2	3	3	4	3	3	2	1	0	3	0	2	1	1	1
Ortho IV	0	0	0	0	0	0	3	0	2	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0
Ortho V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ortho X	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	1	0	0	2	1	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0
Ortho XIV	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Prodiamesinae	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ortho XII	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Ortho XIII	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	2
Procladius	0	0	0	0	0	0	0	1	4	3	0	2	0	0	0	0	2	0	0	0	3	1	2	0	1	1	0	1	0	1	0	0	0	0	0	0
Paramerina	0	0	0	0	1	0	0	2	1	1	1	1	0	1	2	1	0	1	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Tanypodinae I	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0

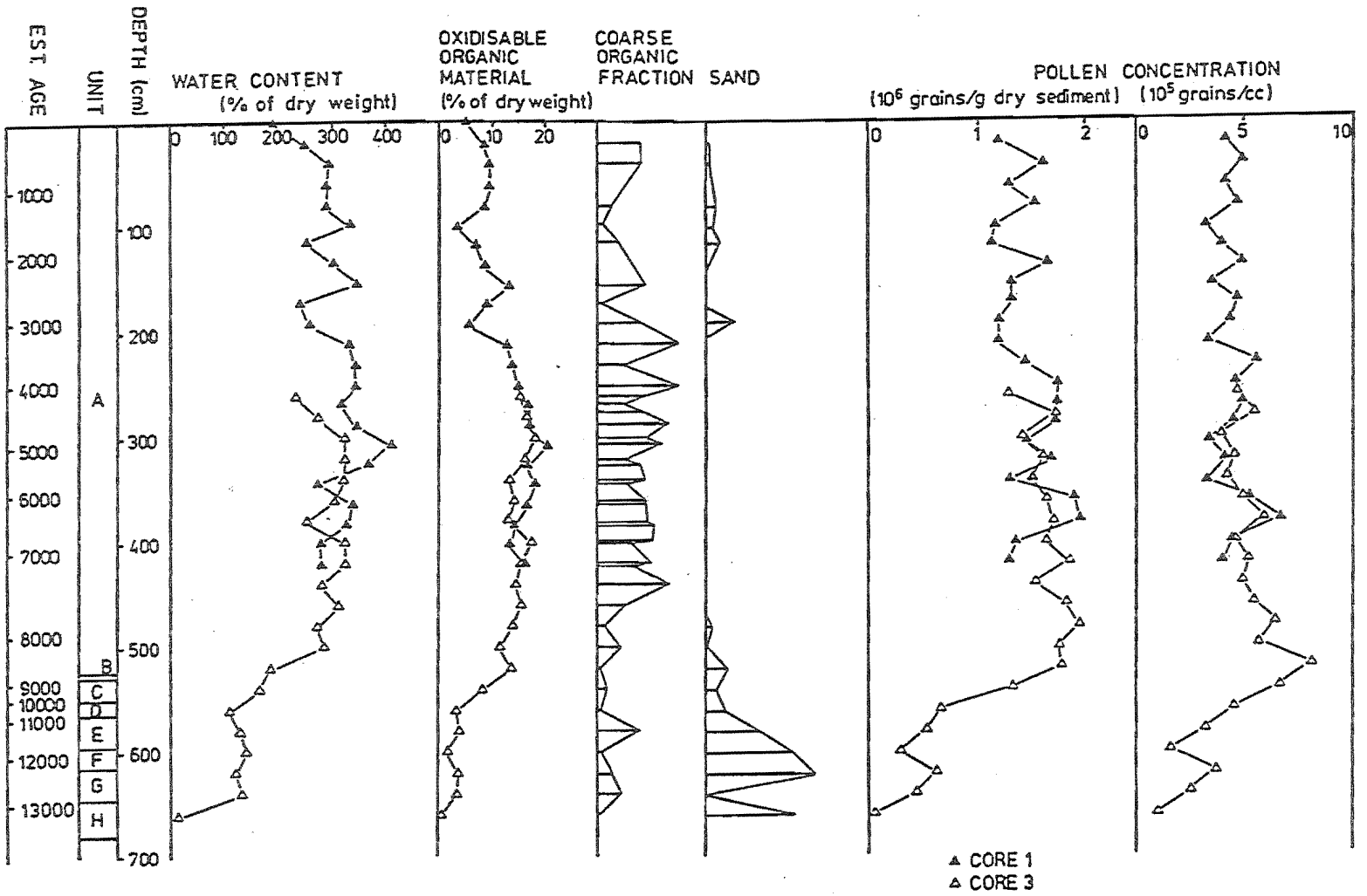


FIG. 3.5 DEPTH PROFILES OF SELECTED SEDIMENT FRACTIONS, BLUE LAKE CORES 1&3 (from Raine, 1974).

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Stratigraphy of the fossil Chironomidae (Diptera) from Lake Grasmere, South Island, New Zealand, during the last 6000 years

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Key words: Chironomidae, Palaeolimnology, New Zealand

Abstract

The fossil chironomid fauna of a 3.26 m long sediment core from Lake Grasmere has been analysed. The fossil chironomid taxa belong mainly to the subgroups Tanytarsini, Orthocladiinae, Chironomini, and Tanyphodinae. Heptagyini and Podonominae were not common. Tanytarsini were the dominant component of the fauna with *Corynocera* sp. as the most abundant species during pre-Polynesian times (before 1000 yr BP). The abundance and the composition of the fossil chironomid taxa have fluctuated markedly over the last 6000 years. These fluctuations could be partly correlated with changes in the stratigraphy of the sediments in the core. Layers of highly minerogenic sediment contained the lowest numbers of remains whereas high abundances were found in the sections of the core with the greatest proportion of organic matter. It is suggested that major shifts in the structure of the chironomid community have been mainly caused by changes in the hydrology and inflows of the lake, and the rate and type of sedimentation, in addition to variations in lake productivity.

Introduction

The analysis of fossil Chironomidae has been of considerable interest to palaeolimnologists especially in the Northern Hemisphere, as emphasised by Hofmann (1988) and Walker (1987). The composition and successional changes of the fossil chironomid fauna have been used mainly to reconstruct past environmental conditions during lake ontogeny. But this type of analysis can also be employed to follow the development of certain taxa and gain information about the structure of chironomid communities over time. This aspect of the study is important for the general understanding of the chironomid communities in New Zealand lakes.

Study area

Lake Grasmere is located in the Cass Basin in the montane region of the Waimakariri River catchment, North Canterbury. The Waimakariri River drains a section of the Southern Alps and the topography of its catchment is the direct result of glacial and post-glacial activity (Hayward, 1967). Lake Grasmere (43° 05′ South, 171° 45′ East) is a small, mesotrophic lake, situated at about 600 m A.S.L. (Stout, 1972). The area of the lake is 0.63 km^2 and its maximum depth is 15 m (Fig. 1). There is one surface inlet stream, and in addition, the waters of Ribbonwood Creek reach the lake as springs after flowing underground through the New Ribbonwood Creek Fan. The recent chironomid fauna is composed of 17 species (Stark, 1981a; Timms, 1982, 1983). This

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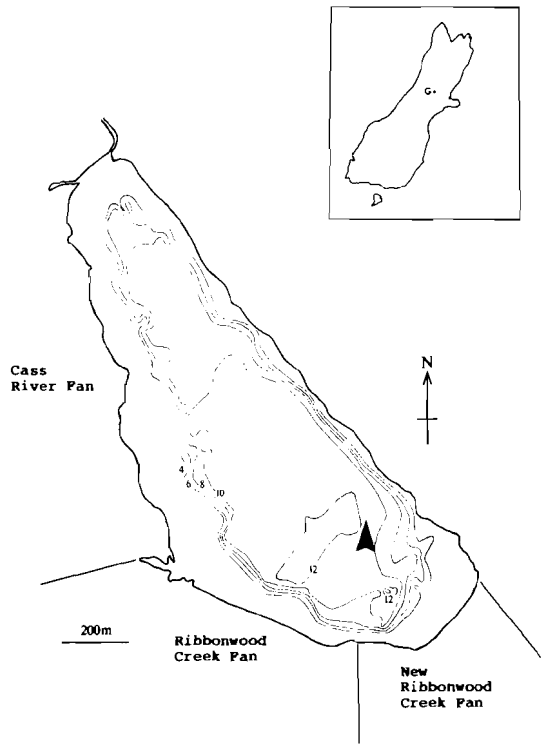

Fig. 1. Bathymetric map of Lake Grasmere (Contour Interval: 2 m). The black triangle indicates the sampling site of the sediment core. The inlet shows the South Island of New Zealand with the location of the lake (G).

is the highest number of species recorded from any New Zealand lake.

Lake Grasmere was formed partly by glacial activity, and partly by alluvial aggradation (Gage, 1959). The ice of the Waimakariri glacier, formed during the last advance of the Otira glaciation, withdrew possibly about 13500 years ago from the Cass area (Burrows, 1978) and Lake Grasmere originated after the ice retreat (Gage, 1959). The lake was partly dammed by ice-eroded rock. The greater part of the lake perimeter is formed by three extensive alluvial fans. The ages of the Cass Fan and the Old Ribbonwood Fan are uncertain, but both might have been deposited during late-glacial times (Soons, 1977). Deposition has still continued in the New Ribbonwood fan in historic times, decreasing the area of the lake. Originally, the lake probably extended eastwards (Gage, 1959).

The development of vegetation after the end of the Otira glaciation in the South Island followed a general pattern from open grassland-shrubland through shrubland to forest (Moar, 1971). Two forest zones could be distinguished in a pollen diagram from Kettlehole Bog, near Lake Grasmere (Lintott & Burrows, 1973). The original forest consisted of podocarps, indicating a climate with mild temperatures and reliable precipitation levels. The present climate at Cass does not allow the growth of these taxa. *Podocarpus* forest remained dominant in the area until at least 7500 yr BP (Moar, 1971). At some time after that, the vegetation changed to a *Nothofagus* (Southern Beech) forest. This transition may represent a change in climate to lower minimum temperatures, greater temperature extremes, lower rainfall and the occurrence of periodic drought (Burrows, 1979).

Pollen analysis of samples of the Lake Grasmere core, carried out by Dr. M. McGlone, showed that *Nothofagus* was already well established by 6000 yr BP in the catchment area of the lake. Most samples were dominated by *Nothofagus fusca* type pollen. An increase of grass pollen at the 30 cm level recorded the arrival of the Polynesians around 1000 years ago (McGlone, 1989). Burning of the forest cover was used by Polynesian hunters in this area especially between 500 and 1000 yr BP (Molloy, 1977). The presence of European settlers was shown by *Pinus* and *Rumex* pollen in the sediments of the core from 6 cm upwards. This means that the last 6 cm of the core were deposited after 1857 when the area was first explored and settled by Europeans (McLeod & Burrows, 1977).

Methods

The sediment core was obtained from Lake Grasmere using a modified hand-operating Livingstone piston corer (Green, 1979). The coring site was located in the southeastern part of the lake at a water depth of 10.5 m (Fig. 1). A total of 326 cm of sediment were recovered. The bottom 6 cm were comprised of medium grey clay

and silt. This layer prevented more sediment from entering the coring tube. In the laboratory, the core was cut in half. One half is stored undisturbed for reference in the Zoology Department, University of Canterbury. The second half was sampled mostly at 10 cm intervals, each sample consisting of 1 ml of wet sediment. Smaller sampling intervals were chosen where changes in the stratigraphy of the sediments were visible. Parallel samples were taken for the determination of dry weight and loss-on-ignition. For the analysis of chironomid remains, the samples were treated with a slightly modified method as described by Boubee (1983) and Walker & Mathewes (1989). New Zealand (Forsyth, 1971; Stark, 1981b), as well as overseas keys (Simpson & Bode, 1980; Wiederholm, 1983) were used to identify the chironomid remains. The interpretation of the results was based on the relative abundance of the chironomid taxa in the samples.

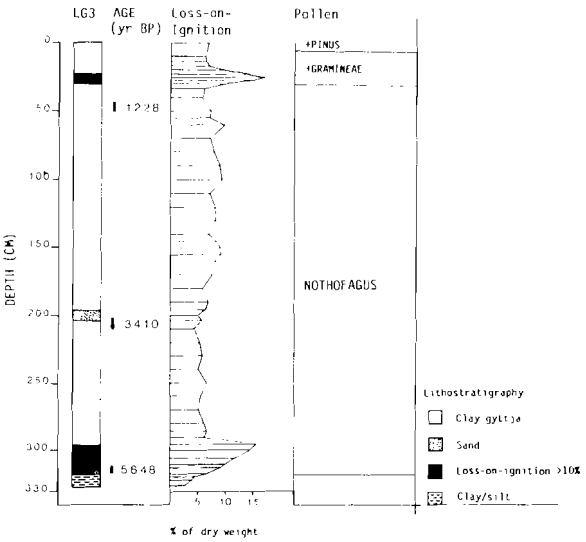

Fig. 2. Summary figure illustrating major features of the sediment core (LG3), the age of the sediments, the results of the loss-on-ignition analysis, and the results of the preliminary pollen analysis.

Results

Sediment record

The Lake Grasmere core consisted mostly of clay gyttja of varying shades of olive grey. A layer between 196 and 204 cm contained sand particles sized from 0.02–2 mm. The bottom 6 cm were dominated by clay and silt (Fig. 2). Results of loss-on-ignition revealed a relatively low content of organic matter in the core with values ranging from 2.5 to 17.7% organic matter dry weight. The organic content throughout most of the core remained relatively stable, the only fluctuations being a minimum of 2.5% at the base and two pronounced maxima at the 315 and 25 cm horizons.

Radiocarbon dates are presented in Table 1. The date from the oldest sediments (at 318 cm) revealed that the sediment core from Lake Grasmere spans nearly 6000 years and might not cover the entire history of the lake. The clay/silt layer at the base of the core might have been deposited during a period of naturally accelerated erosion (Grant, 1985). Erosion and sedimentation occurring in the mountainous regions of the South Island are very high and sediment yields from some basins in the Southern Alps are amongst the highest in the world (Griffiths, 1981, Whitehouse, 1984). Possible causes for increased rates of sediment transport include increased flood flows produced by a greater frequency and/or magnitude of rainstorms (Beschta, 1983; Grant, 1985) possibly in connection with damage to vegetation by fire. The fine sediment at the base of the Lake Grasmere core might have been trasported into the lake via Ribbonwood Creek or the Cass River. The Cass River could have been an inflow of Lake

Table 1. Radiocarbon dates for samples taken from the Lake Grasmere core.

Core depth (cm)	Laboratory number	Date
310–318	NZ–7568	5648 ± 200 yr BP
202–210	NZA–353	3410 ± 120 yr BP
42– 50	NZA–349	1228 ± 69 yr BP

The radiocarbon-dating was carried out by the Institute of Nuclear Science, Wellington, New Zealand.

Grasmere 6000 years ago as the form of its fan shows. A possible explanation of the origin of the clay/silt layer is that a series of frequent large rainstorms in the Craigieburn Ranges, where the headwaters of Ribbonwood Creek and the Cass River are located, caused severe hillslope erosion. Subsequently, sediment masses were transported downstream, the coarser sediments were deposited in the fans and at the lake margin, and the fine sediments finally in the deeper parts of the lake. The strongly increased sediment influx had a pronounced influence on the chironomid fauna as will be shown later.

Chironomid stratigraphy

The chironomid analysis was based on 56 subsamples, each consisting of 1 ml of sediment. For the analysis, absolute numbers of chironomid head capsules per volume unit were counted. A total of 5290 head capsules was retrieved averaging 96 remains per ml of sediment. The abundance of chironomid remains in the core fluctuated considerably (Fig. 3). These fluctuations could be partly correlated with changes in the stratigraphy of the core. Layers of highly minerogenic sediment contained the lowest numbers of remains whereas two peaks of higher abundance were found in the sections of the core with the highest proportion of organic matter. The greatest maximum abundance at the 150 cm level was not connected to any special sediment features.

Five chironomid subfamilies occurred in Lake Grasmere. Head capsules belonging to the Heptagyini and Podonominae were rare. Tanytarsini were the most abundant subgroup with a relative abundance of 37.3%, Chironomini were the sub-dominant group with 25.5%, Tanypodinae occurred with 17.9%, and Orthocladiinae with 15.8% relative abundance.

Comparing the relative abundances of the four main chironomid subgroups in Fig. 3, it is clearly shown that Tanytarsini represented the dominant form of the fossil chironomid fauna during most of the lake's developmental history under study.

Orthocladiinae showed a peak in dominance in the younger sediments between 10 and 30 cm. The Chironomini were important throughout the core but were especially dominant in the upper-

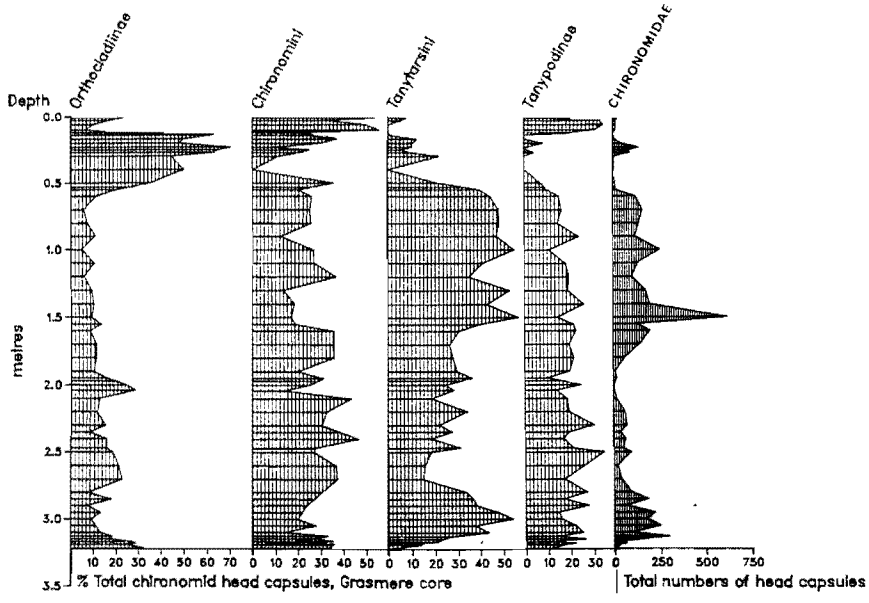

Fig. 3. Lake Grasmere: Total number of chironomid remains and the relative abundance (% of sum at each level) of the main chironomid subgroups in the samples of the core.

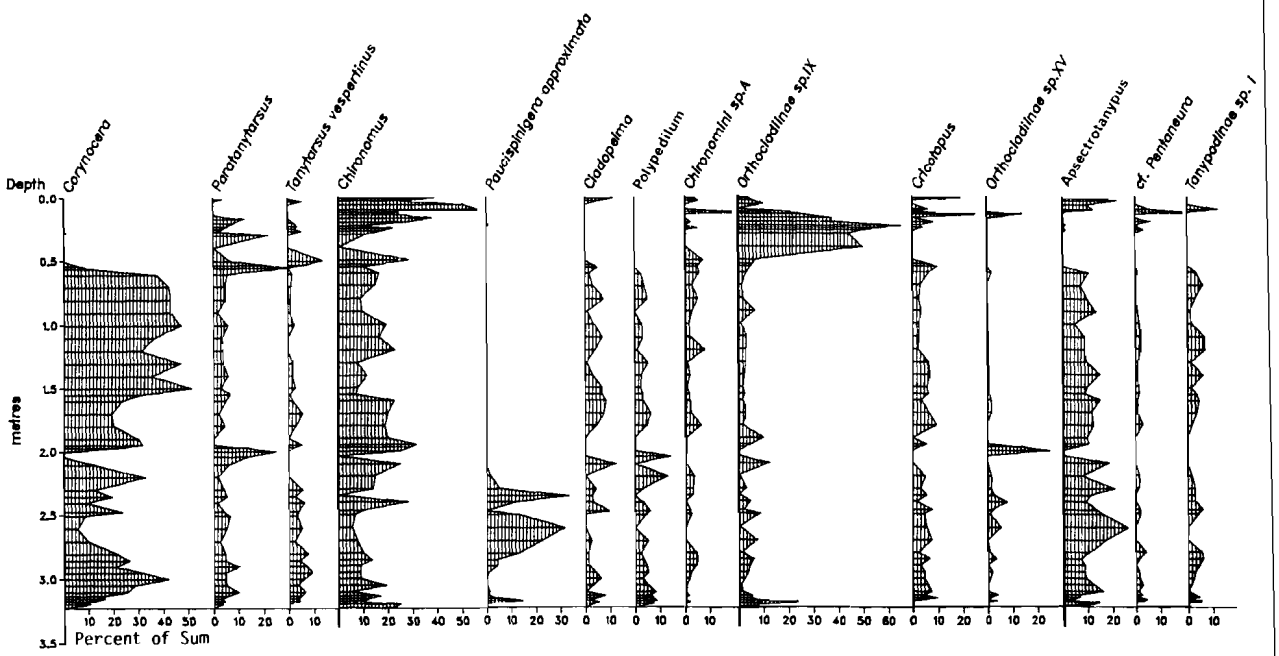

Fig. 4. Percentage diagram of the most abundant chironomid taxa for Lake Grasmere (percentages are calculated as proportion of all chironomid head capsules counted in each sample).

most samples. The relative abundance of Tanypodinae remained stable in most samples, except for a minimum in the more recent sediments.

The fossil chironomid remains from Lake Grasmere could be distinguished in terms of 35 taxa, but only 14 occurred with a relative abundance higher than 1% of the total number (Fig. 4). Chironomini and Orthocladiinae were the most diverse subgroups with 11 taxa in each. *Chironomus* (13.7%) was the most important Chironomini taxon. The number of undescribed taxa (6) in the Orthocladiinae was high owing to the poor taxonomic knowledge of this group in New Zealand. Orthocladiinae sp. IX (7.1%) was the most abundant taxon in the Orthocladiinae. In the Tanytarsini, only four taxa could be distinguished. *Corynocera* constituted the most dominant, with 28.8% relative abundance. The most abundant Tanypodinae head capsules belonged to *Apsectrotanypus* (9.3% relative abundance). Six Tanypodinae taxa were separated.

The temporal distribution of the chironomid taxa in the Lake Grasmere core showed some significant trends (Fig. 4). The dominant chironomid, *Corynocera*, appeared in low abundance in the top sample of the basal clay/silt layer, and became the dominant form in most samples from 310 cm up to the 55 cm level. In the youngest sediments (50 cm to the top of the core), and in two samples of the sandy layer (200–204 cm), *Corynocera* was not found. This taxon occurred in low numbers at the 260 cm horizon. The abundance of *Chironomus* fluctuated strongly in the core but the taxon was an important part of the fauna in nearly every sample. A pronounced peak in abundance of *Chironomus* occurred in the youngest sediments of the core. Orthocladiinae sp. IX occurred during the entire period covered by the core in relatively low abundances, but became the dominant chironomid taxon in the sediments between 12 and 40 cm. In the sample at the 23 cm level, 65.5% of all head capsules found belonged to this taxon.

Discussion

The sediment core from Lake Grasmere covered the last 6000 years of the lake's developmental history. All sediments in the core were deposited during the *Nothofagus* phase of the Holocene. During this period, no major climatic change occurred. Therefore, it is unlikely that influences of macroclimate (e.g. a major change in temperature) would have been the cause of changes in the faunal composition of the fossil chironomids of Lake Grasmere.

Factors to which variations in the chironomid fauna might be attributed include the trophic state or the productivity of the lake, the oxygen concentration of the hypolimnion (Brundin, 1951; Hofmann, 1978), and the quality and availability of food (Sæther, 1979; Kansanen *et al.*, 1984). Warwick (1980) emphasized the significance of sedimentation processes.

The interpretation of the observed changes in the subfossil chironomid associations of Lake Grasmere presents some difficulties. Two factors restrict a detailed analysis of the faunal succession and its ecological significance: the relatively high number of undescribed or previously unknown taxa (especially in the Orthocladiinae and Tanypodinae), and the rather sparse ecological information available for many chironomid species in New Zealand. However, the existing information about various fossil chironomids from Lake Grasmere makes it possible to reconstruct some aspects of the lake's history.

It is suggested that some pronounced shifts in the structure of the chironomid community have been mainly caused by changes in the hydrology and the inflow of the lake and by variations in the rate and type of sedimentation. Changes in lake productivity as well had an influence on the fossil chironomid fauna.

The clay/silt layer at the base of the core represented a major environmental disturbance for the bottom fauna of the lake. The massive input of fine mineral sediments was carried into the lake either by Ribbonwood Creek (in which case the waters of the creek must have entered the lake as a surface inlet), or the Cass River, and must have caused high turbidity. The rapid mineral sediment accumulation appears to have eliminated the profundal fauna. The sample at the bottom of the core consisted almost entirely of clay and silt particles.

The first chironomid remains were found at 322 cm. Initial numbers were low and included only five taxa. The change in sediment consistency to organic clay mud at the 318 cm level indicated the termination of the high sediment input, followed by clearing lake waters. Numbers and diversity of chironomids increased rapidly in correlation with a possible rise in lake productivity about 5500 years ago, as indicated by the relatively high organic content of the sediments.

Corynocera, the dominant subfossil chironomid in Lake Grasmere, can be used as an indicator of a distinct substrate type. Larvae of *Corynocera* were found in lakes of the Waikato region (Boubee, 1983) which had clear water with a maximum water depth of 1 m. The sediments consisted of a flocculent organic layer with a high concentration of algae (mainly diatoms). Boubee (1983) considered *Corynocera* to be an indicator for low water levels and Deevey (1955) found exceptionally high numbers (1500 hc/ml sediment) of this genus in Pyramid Valley lake which was shallow throughout its history. But the consistency of the substrate appears to be a more important factor than the water level influencing the distribution of *Corynocera*. Timms (1983) recorded *Corynocera* from Lake Letitia, near Cass, where larvae of this type were abundant down to a water depth of 12.5 m. Timms (1983) noted the special consistency of the mud which was 'brown, very soft, and composed largely of small aggregates of flocculent material' (p. 46). In the sediments of the Lake Grasmere core, *Corynocera* occurred in high abundances when sedimentation processes remained stable.

Visible changes in the sediment of the core were correlated with low abundances or the absence of *Corynocera*. At the 260 cm level at 1 cm wide dark lamination was noted. In this sample, the abundance of *Corynocera* declined to a minimum comparable to that in the older sediments of the core. The nature of the sediment changed considerably

at 204 cm. The following 8 cm contained a relatively large amount of sand particles. Such sand deposits can accumulate as a result of unusual storms which produce sufficient water currents and wave action to move material out from the shore (Davies & Moeller, 1985). This is the most probable cause for a high country lake in the South Island. Grant (1989) suggested that in New Zealand periods of increased storminess, erosion and alluvation, caused by changes of atmospheric circulation, alternated with tranquil intervals when erosion and sediment transport declined and soil formed. Head capsules of *Corynocera* were not found in the samples derived from the sandy layer of the core but this taxon occurred again in a relatively high abundance at 195 cm immediately after the deposition of sand had ceased. Many of the other taxa of the chironomid community responded negatively to the disturbance, and numbers of head capsules and taxa declined considerably in this sediment layer.

For about the next 1500–1800 years (195–60 cm) *Corynocera* occurred in high abundances indicating a stable environment. The composition of the entire fauna remained relatively constant.

In the most recently deposited sediments of the core (55 cm-surface), a major shift in faunal composition was recorded. *Corynocera* disappeared entirely, suggesting a sedimentation – related disturbance. At 55 cm, numbers of chironomid remains as well as taxa, declined a suddenly although no apparent change in the sediments of the core was discernible. A colour change and an increase of organic matter in the core occurred between 30 and 22 cm. The succeeding sediments consisted of a sequence of alternating pale and light olive grey, implying a rapid change in sedimentation pattern during the last 1000 years.

At this stage of the study, it is not possible to determine the exact mechanism which governed the sudden change in the faunal composition at the 55 cm horizon. A possible explanation could be a change in the lake area caused by encroachment of the New Ribbonwood Fan. As mentioned earlier, deposition in the fan still continued in historic times (Gage, 1959). Another factor which added to the instability of the environmental conditions of the lake during the last 1000 years was the appearance of the first Polynesians, in particular their influence on the landscape of the Cass Basin through use of fire (McGlone, 1989; McSaveney & Whitehouse, 1989). The increase of grass pollen at the 30 cm level in the core correlates with the maximum in organic matter and the pronounced peak in the abundance of Orthocladiinae sp. IX. This high abundance might indicate a rise in lake productivity as well as increased input of allochthonous material caused by the frequent fires in the early period of Polynesian settlement. Undescribed larvae of this genus have been found also in shallow ponds in the Botanic Gardens, Christchurch (pers. obs.) where they occur in large numbers. These ponds have a high density of macrophytes and also receive a high influx of allochthonous organic matter.

Towards the top of the core, the abundance of Orthocladiinae sp.IX decreases and *Chironomus* becomes the dominant chironomid. The top most 6 cm of the core cover the time of European settlement in the area and the dominance of *Chironomus* indicates a slight shift towards mesotrophy (Graham, 1976; Forsyth, 1986; Schakau, 1986).

In summary, the conditions in Lake Grasmere have changed considerably during the last 6000 years. Long periods with a relatively stable environment, reflected by high abundances of certain chironomid taxa and a comparatively unchanging faunal composition, were disrupted by short-term but high magnitude disturbances resulting in a decline of chironomid diversity and abundances and shifts in community structure. The subfossil chironomids from Lake Grasmere are good indicators of the general changes which have occurred in this geologically active environment of the Southern Alps of New Zealand.

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Preliminary study of the development of the subfossil chironomid fauna (Diptera) of Lake Taylor, South Island, New Zealand, during the younger Holocene

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Keywords: paleolimnology, chironomidae, subfossil remains, Aranuian, lake Taylor

Abstract

The composition and succession of the subfossil chironomid fauna has been studied in a sediment core from Lake Taylor. The sediments of the core are all within the *Nothofagus* phase of the last 3000 years within the Aranuian. In the older sediments of the core the chironomid fauna was dominated by Tanytarsini and Orthocladiinae whereas Chironomini dominated in the more recent sediments. The species diversity is very high compared with the results of other studies of the recent chironomid fauna of lakes in the South Island. The most abundant head capsules belong to the taxa *Chironomus zealandicus, Tanytarsus vespertinus, Corynocera* sp., and *Eukiefferiella* sp. Several additional taxa which have not yet been described also occurred in large numbers. It is not possible to correlate any definite changes in the composition of the subfossil chironomid fauna with a change in climatic conditions or the trophic status of the lake.

Introduction

In North America and Europe, analyses of subfossil chironomid remains from lake sediments have proved to be a useful paleolimnological technique for indicating the changes of limnological conditions during the developmental history of lakes. In New Zealand, there exist only two paleolimnological studies. Deevey (1955) analysed a short core from the Pyramid valley upper swamp deposit in the South Island without a detailed chironomid analysis. Boubee (1983) studied the developmental history of Lake Maratoto, North Island, using chironomid remains. The results of his study showed a succession of the subfossil chironomid fauna as a response to changes in the typological development of the lake.

The intention of my study has been to gain information about the distribution and succession of chironomid taxa in the past of South Island lakes.

Study area

Lake Taylor (Fig. 1) is one of the high country lakes of the upper Hurunui valley, North Canterbury. The lake is at latitude of 42° 46′ South, longitude 172° 14′ East. The area of the upper Hurunui valley was greatly influenced by the last glaciation (the Otira) and L. Taylor has existed since the end of the Poulter advance – the last glacial advance of Otira – which came to an end about 14000 years B.P. (Suggate 1965). The lake has an area of approx. 1.85 km^2 and a maximum depth of 40 m (Irwin, 1975). The chemical quality of the lake is typical of Canterbury high country lakes: low in major ions and low in nitrogen and phosphorus. As stated by previous studies, the trophic status of the lake rangés between oligotrophic and mesotrophic (Bowden, 1977). Thermal stratification did not occur during previous sampling programmes.

Additionally, short sediment cores from Lake Monowai, one of the deep, cold, and oligotrophic lakes in the south of the South Island, and from Lake Grasmere in the Waimakariri River catch-

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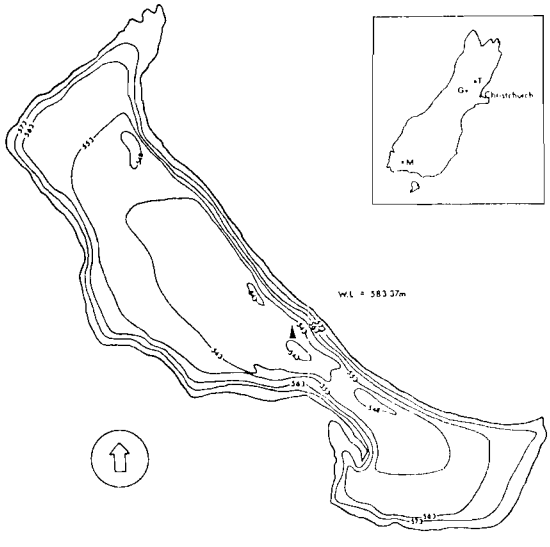

Fig. 1. Lake Taylor: Bed contours, (m.s.l.), scale 1:150 000. The black triangle indicates the sampling site of the sediment core. The inlet shows the South Island of New Zealand with the location of the 3 studied lakes (M = Lake Monowai, G = Lake Grasmere, T = Lake Taylor).

ment, have been studied to provide material for a comparison of different subfossil chironomid communities (Fig. 1).

Material and methods

The sediment core of Lake Taylor was sampled by the Oceanographic Institute, Wellington, using a Hunt piston corer. The sampling site was in mid-lake at a water depth of 37 m. The 1.85 m long core was subsampled at 10 cm intervals, each subsample consisting of 1 ml dry sediment. For the determination of chironomid remains, the subsamples were treated as described by Boubee (1983). Both New Zealand identification keys (Forsyth, 1971, Stark, 1981b) and overseas keys (Hofmann, 1971, Oliver *et al.*, 1978, Wiederholm, 1983) were used to identify the chironomid remains. The interpretation of the results was based on the relative abundance of the chironomid taxa in the subsamples.

The composition of the subfossil fauna in the subsamples was compared by using Sørenson's (1948) Quotient of Similarity. Afterwards, a cluster analysis was carried out (Southwood, 1966).

According to the radiocarbon dating, the oldest sediments of the core were deposited 3000 years B.P. (Institute of Nuclear Science, Wellington, File CA/4/1). A pollen analysis showed that all studied samples were dominated by *Nothofagus fusca* type pollen and all sediments of the core came within the *Nothofagus* phase of the Aranuian.

The Aranuian (Suggate & West, 1967) began with the first warming after the last glacial advance and corresponds with the late- and postglacial period in Central Europe. During the Aranuian, the succession of vegetation in different South Island districts was through grassland-shrubland to shrubland and then to forest with a succession from *Podocarpus* to *Nothofagus* forest (Burrows, 1979). There exists no pollen diagram of the Hurunui catchment but present evidence indicates that *Nothofagus* spread in the Waimakariri valley approx. 6000 years B.P. (Moar 1971) and the same timing may apply in the Hurunui valley (Moar, pers. comm.).

Results

A total of 1831 chironomid head capsules representing 40 taxa was identified from the 20 subsamples of the Lake Taylor core. The total number in the subsamples varied between 21 to 196 head capsules with an average of 91 head capsules/ml dry sediment. The Tanytarsini were the most important subgroup with 30.5% relative abundance, followed by the Chironomini with 27.5% and Orthocladiinae with 25.7%. Tanypodinae occurred with a relative abundance of 10.5% and Podonominae with only 0.2%.

The abundance of chironomids showed strong fluctuations (Fig. 2) but in the older sediments of the core (from 185 cm to 110 cm), the number of head capsules was generally larger than in the more recent sediments, and the chironomid fauna was dominated during these times by Tanytarsini and Orthocladiinae whereas a slight domination of Chironomini took place from 70 cm up to the top of the core.

Of the 40 taxa distinguished, 18 taxa belong to yet undescribed species. The head capsules of these taxa make up 27% of the total number of chironomid remains. Only 5 taxa of the 18 distinguishable Orthocladiinae taxa could be identified to generic level. Thus, 15% of the Orthocladiinae head capsules were not determinable. In the sub-

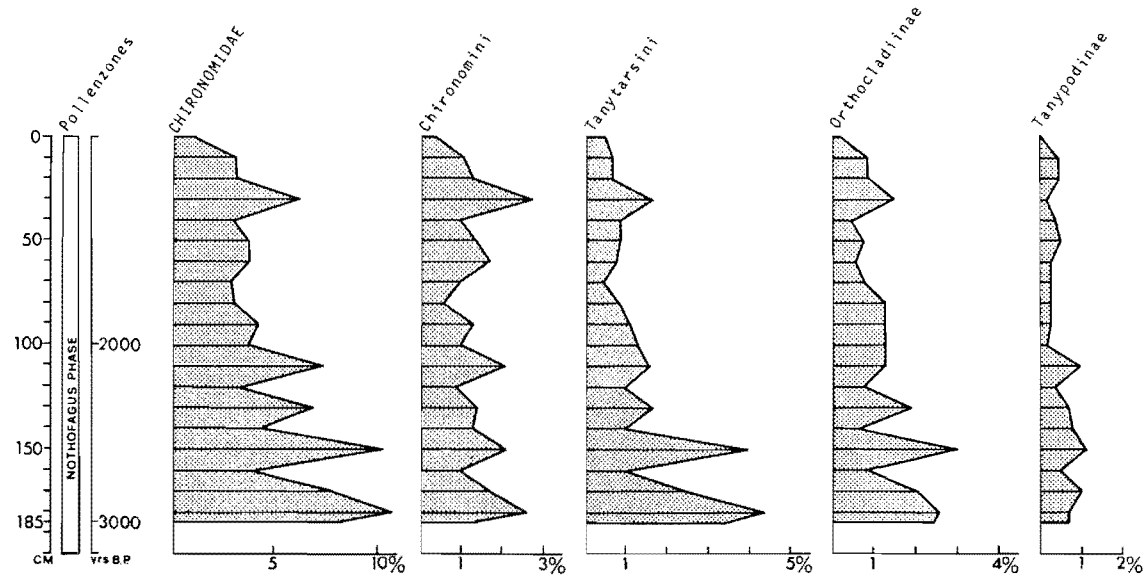

Fig. 2. The relative abundance (% of the total number) of total chironomids and chironomid subgroups in the sediment core of Lake Taylor. Radiocarbon dating according to the Institute of Nuclear Science, Wellington.

group Tanytarsini. 2 of the 8 taxa were undescribed, 7.7% of the Tanytarsini remains belonged to these 2 taxa. 4 undescribed Chironomini taxa were found in the relative abundance of 4.6%. A total number of 11 Chironomini taxa was distinguishable. Tanypodinae presented the greatest taxonomic difficulties; most of the head capsules were too much fragmented to make an identification possible, except for some head capsules which belong to *Macropelopia umbrosa, Gressittius antarcticus* and *Psectrotanypus* sp.

The most abundant chironomid genera (Fig. 3) were *Chironomus zealandicus* (14.7%), *Tanytarsus vespertinus* (14.0%), *Corynocera* (7.5%), *Eukiefferiella* (4.0%), *Cricotopus* (3.7%), and *Paucispinigera* spec. a (3.3%). Some of the undescribed taxa occurred in quite large numbers, e.g. Chironomini A (4.0%), Tanytarsini A (7.5%), and Orthocladiinae A (3.5%). The relative abundance of 26 taxa was smaller than 1% of the total remains. Some of the rare taxa were *Cladopelma, Calopsetra funebris, Stempellina, Synorthocladius* and *Corynoneura. Stempellina* and *Synorthocladius* are not yet recorded in New Zealand. I identified these taxa with the help of overseas keys.

The subfossil chironomid fauna of Lake Grasmere consisted of 24 taxa (incl. 6 undescribed taxa). Tanytarsini were the main component of the fauna with a relative abundance of 35%. The dominant taxa were *Corynocera* sp. (29%) and *Chironomus zealandicus* (19%). The composition of the subfossil chironomid fauna of Lake Monowai differed from those of both North Canterbury lakes. A total number of 30 chironomid taxa was determinable (incl. 7 undescribed taxa). Orthocladiinae were the dominant component of the fauna (52% relative abundance). Tanytarsini occurred only with a relative abundance of 5%. The so far highest percentage of Podonominae (8.8%) was found and 2% Diamesinae head capsules. The composition of the subfossil chironomid fauna of Lake Monowai with the higher percentage of Orthocladiinae and Podonominae, which are more cold adapted taxa, resembles the composition of the Chironomidae fauna of New Zealand's subantarctic islands (Sublette & Wirth, 1980).

Discussion

Most of the dominant taxa of the subfossil chironomid fauna of Lake Taylor were distributed relatively regularly in the core. *Chironomus zealandicus* appeared in nearly every subsample in high

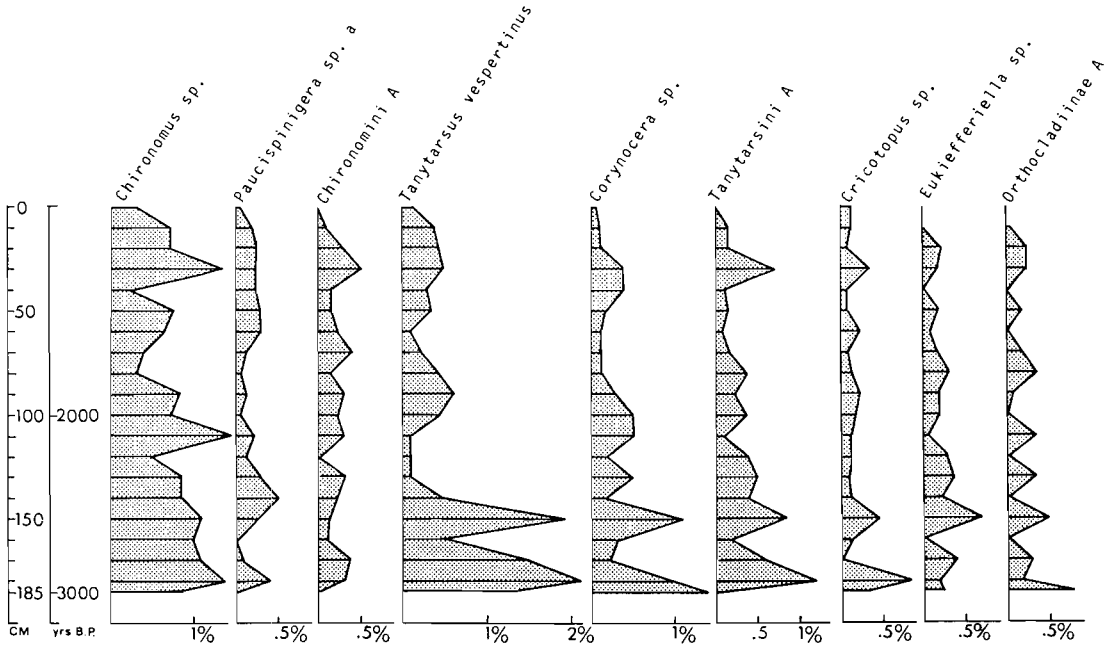

Fig. 3. The relative abundance of dominant chironomid taxa in the sediment core of Lake Taylor.

abundance whereas all 3 dominant Tanytarsini taxa had their maximum abundance in the older sediments and then decreased in numbers. Except for a slight shift in dominance from Tanytarsini to Chironomini in the last 2500 years, the composition of the chironomid fauna remained stable throughout most of the last 3000 years of the developmental history of Lake Taylor. The cluster analysis dendrogram of the 20 subsamples (Fig. 4) based on Sørenson's Quotient of Similarity sug-

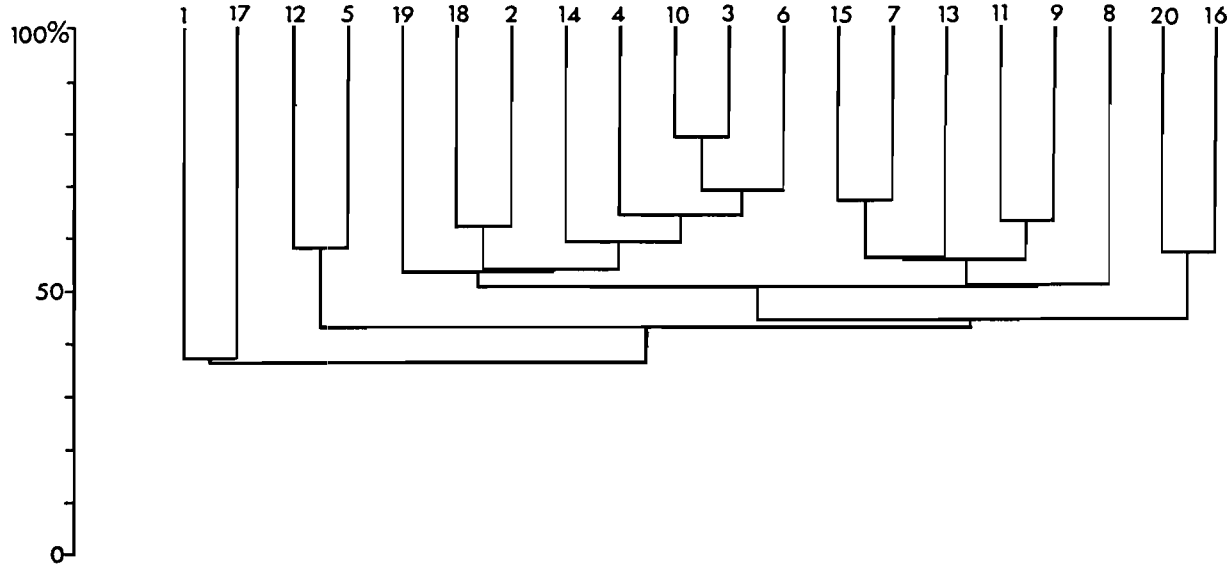

Fig. 4. Dendrogram showing the result of the Cluster analysis of the 20 subsamples on the abundances of the subfossil chironomid taxa. The vertical axis gives the percentage values of Sørenson's Quotient of Similarity. The horizontal numbers indicate the numbers of subsamples (1 = subsample from the top of the core, 20 = subsample from the bottom).

gests that there is no faunal zonation. Therefore, it is not possible to correlate any definite changes in the composition of the subfossil chironomid fauna with a change in climatic conditions of trophic status of the lake.

It can be suggested that in comparison with the composition of the subfossil chironomid fauna of oligotrophic Lake Monowai, the relatively high percentages of Chironomini and Tanytarsini of Lake Taylor, especially *Chironomus zealandicus,* indicate a mildly-mesotrophic to mesotrophic status of the lake throughout the last 3000 years of the latter's history. The subfossil chironomid fauna of mesotrophic Lake Grasmere was also dominated by Chironomini and Tanytarsini, with *Chironomus zealandicus* as the dominant component of the fauna in the more recent sediments. *Chironomus zealandicus* can sustain quite low oxygen concentrations and has high abundances in highly productive lakes (Graham, 1976).

It can be regarded as a main result of my study that the species richness of the chironomid fauna of the South Island appears to be much higher than it had been stated before (Timms, 1982, compare also with Stark, 1981a).

Although the high number of undescribed species restricted the analysis of subfossil chironomids, this type of analysis could encourage further searches for living larvae of these species and, therefore, lead to an increase of the taxonomic and ecological knowledge of New Zealand's Chironomidae.

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